SIGMA XI QUARTERLY

*A quarterly publication of the Society of the Sigma Xi devoted to the promotion of Scientific Research*

VOL. XXIX JULY, 1941 NO. 2

# SOME FUNDAMENTAL ASPECTS OF PHOTOSYNTHESIS

By J. FRANCK

University of Chicago

IT is generally known to scientists that photosynthesis is the synthesis of organic matter in green plants with the help of the sunlight, and that this process is the only source of organic matter existing on earth. However, this simple statement contains many premises taken from the field of physical chemistry which must be discussed.

Organic matter consists of carbon, hydrogen, some oxygen, and often additional elements in smaller proportions. To answer the question of why organic matter is not formed on the earth without photosynthesis it is necessary to explain why it cannot be formed through the agency of heat energy alone. The atmosphere of the earth was exceedingly hot when our planet was being formed, and at such high temperatures most chemical compounds cannot exist but, rather, are dissociated into free atoms. Slowly the earth cooled and the compounds were formed which are found, for instance, in the solid crust of the earth. Organic matter was, of course, also formed at that time as an intermediate product. But since all organic matter is oxidized in the presence of oxygen, and heat is liberated in the course of this reaction, we conclude that at high temperatures organic matter is not a stable configuration of carbon, hydrogen, and oxygen. The organic matter formed at high temperatures will, therefore, be shortlived and will combine with oxygen to form stable products, such as carbon dioxide and water.

The geologist and mineralogist have thus come to the conclusion not only that organic matter was absent as the crust of the earth was slowly formed, but also that oxygen was practically absent from the atmosphere. The conditions which prevail now, wherein our atmosphere contains about 20 per cent oxygen, are, like the production of organic matter, the result of photosynthesis.

The next question which arises is why organic matter, once it has been produced under the influence of light, is stable enough to make life possible at the low temperatures now prevailing on earth. Why, for instance, does not the organic matter of which our bodies consist immediately react with oxygen to form carbon dioxide and water? A similar question arises also in the case of inorganic substances. For instance, we know that a mixture of illuminating gas and oxygen can be prepared which is entirely inert at low temperatures. To start the oxidation one has to initiate the reaction by heating a small part of the gas or igniting it with a match, a spark, or similar device. Why does the reaction have to be initiated? The answer is that the molecules have to come very close together before the reaction can begin; they do not come very close together if they collide with one another at low temperatures because the velocities are small and at close range the molecules repel each other. The exact nature of these repelling forces is now explained by modern quantum theory. By raising the temperature the force of the impacts is increased, since the kinetic energy of the atoms and molecules rises proportionately to the absolute temperature. The greater the relative kinetic energy of the colliding particles, the more they can penetrate into the mutual spheres of repulsion, and the nearer the centers of gravity will approach each other; thus, the reaction will start. In the case of reactions which release energy, like the burning of illuminating gas, the energy liberated will raise the temperature of the surrounding gas and therefore activate it; thus, the reactions will spread throughout all of the gas present. One uses the term "heat of activation" to describe the phenomenon discussed. The term "potential barrier" or

"potential wall" is also used in analogy to mechanical processes.

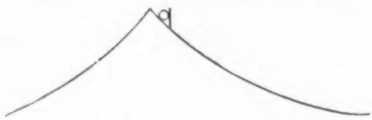


FIG. 1. A "potential barrier" prevents the stone from falling down the hill.

Figure 1 may represent a mountain, and a stone brought close to the top is said to possess potential energy which will go over into kinetic energy and, eventually, into heat as the stone rolls down the mountain to the lowest point. If a little wall is built on the slope of the mountain at the point where we deposited the stone, then some energy will be required to lift the stone to the top of the wall before it can fall down. Just so it is necessary to put in some energy to overcome the initial starting resistance of the chemical reaction. There are reactions with a great heat of activation—a high potential wall—and reactions with small ones.

Following the mechanical analogy, one can use energy diagrams. In Figure 2 the lower level on the right side may represent a stable modification of a chemical compound; the higher level to the left an unstable one. We may, in this instance, let the higher level represent organic matter plus oxygen, and the lower level represent carbon dioxide plus water. The transition from the higher level to the lower level can proceed only over the top of the potential barrier; and, since the particles do not possess enough kinetic energy at low temperature to overcome this barrier, the reaction will not start and the organic matter will be stable in the presence of oxygen. However, this principle alone is not enough to explain why life is possible, because we know that food is burned in the human or animal body to develop the energy necessary for the processes of life and it has to be done at the low temperatures prevailing, for instance, in the human body. All these oxidation reactions are accomplished with the help of catalysts which, when associated

FIG. 2. A potential barrier prevents an unstable compound from going over to a more stable form.

with life processes, are known under the name of enzymes. Many vitamins belong to this group. A catalyst is a chemical substance which, when added in small concentrations to the reaction mixture, activates the reaction without being used up itself. A catalyst may enter into a chemical reaction itself, but it is finally restored unchanged by a second chemical reaction. By its presence, therefore, instead of a reaction which has a high heat of activation, two or more partial reactions occur, each of which has a small heat of activation and can, therefore, proceed at lower temperature as illustrated in Figure 3.

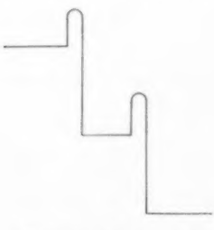


FIG. 3. Action of a catalyst.

Let us take a simple example. Suppose a molecule $A_2$ to react with molecule $B_2$ to form 2AB. This reaction may have a great heat of activation and may not proceed, therefore, at room temperature. However, if a third substance, $C_2$, is added the partial reaction $A_2 + C_2 \rightarrow 2AC$ and $2AC + B_2 \rightarrow 2AB + C_2$ may occur. If both of these have a small heat of activation, they can occur at low temperature. In that case $C_2$ acts as a catalyst. Its presence promotes the reaction without the destruction of $C_2$. Since each catalyst molecule can be used over and over again a small concentration of catalyst molecules is all that is needed. The total reaction will proceed just as fast as the catalyst molecules go through their own reaction cycle.

This discussion may be sufficient to give an understanding of why organic matter can serve as food and be slowly oxidized at the low temperature prevailing in the animal body. Indeed, there are many catalysts connected with the oxidation process in living tissue, and each reaction step develops so small an amount of energy that the other surrounding molecules are not activated—contrary to the behavior in the burning of illuminating gas mentioned above.

Next, we should discuss why light energy alone is especially suited to reverse the process of burning in producing organic matter and oxygen by the combination of carbon dioxide and water. It has been mentioned that the use of

heat energy is unfavorable because the organic matter, once made, will be burned up again. But when visible light is absorbed by a cold gas, the individual molecules take up one quantum of energy at a time, an amount which is several hundred times larger than the energy of thermal motion. This energy can be used to reduce $CO_2$ and $H_2O$, producing organic matter. Furthermore, the freshly formed products remaining in the environment do not burn up because the temperature is too low. The energy amounts given by absorption-acts to the individual molecules depend upon the color of the light. With red light the energy is about one hundred times as great as that due to temperature movement at room temperature. With blue it is nearly two hundred times as large; and with ultra-violet it is even larger. In accordance with the quantum theory, light is emitted and absorbed in energy units, the magnitude of which is proportional to the frequency of the light and, therefore, indirectly proportional to the wave lengths.

It will not be possible to discuss the experimental proofs for the quantum theory, and I shall confine myself to one experiment which has a direct bearing on the problem of photochemistry. Light energy can be used for photochemical processes only if it is absorbed. If this postulate of the quantum theory is correct, we can predict what is to be expected for such simple photochemical reactions as photodissociation of diatomic molecules. The behavior of iodine may be taken as an example, since iodine is a gas which absorbs light throughout virtually the whole visible spectrum. Moreover, from many thermo-chemical experiments, the exact amount of enrgy necessary to dissociate an iodine molecule into two iodine atoms is known. Let us irradiate a bulb containing iodine vapor with monochromatic light and change the wave lengths from the direction of the long wave length region, red and infra-red, to the short wave length region, blue and ultra-violet. No dissociation processes will take place by irradiation in the long wave length region, regardless of the intensity of the light. But on going over to shorter wave lengths, we certainly shall have the

occurrence of dissociation processes at the very moment when the size of the quantum absorbed becomes equal to the heat of dissociation of the iodine molecule. It can be shown that, in this case, all the energy will be used for the dissociation processes. The gas will not become warmer if the recombination of the atoms is hindered. As further progress is made into the short wave length region, the quanta become larger than the heat of dissociation—only a part of the energy may be used for the dissociation process, the rest being dissipated into the temperature movement. The use of energy for the dissociation process plotted as a function of the frequency will then show a curve like that of Figure 4; the yield will be zero until the critical threshold is reached; at the threshold the maximum yield will be obtained, and from then on the yield per unit of energy absorbed will fall slowly. This is actually the behavior observed in many photochemical reactions.

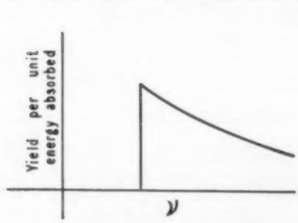


FIG. 4. Curve showing the variation in the number of molecules photolyzed per unit of radiant energy absorbed, as a function of the wave length.

In applying the basic laws of photochemistry to the processes of photosynthesis, we have to consider the fact that only visible light is available for this process. In the infra-red the quanta are too small to be of any value for the production of organic matter, while the ultra-violet emitted by the sun will not reach the surface of the earth because it is absorbed in the higher levels of our atmosphere by the ozone formed photochemically in these layers out of oxygen. But visible light is not absorbed by either carbon dioxide or by water, since neither shows any color. To reduce carbon dioxide photochemically a dyestuff is needed which absorbs the visible light and transfers the energy to the carbon dioxide and water. Reactions of this type are called sensitized photochemical processes. The essential dyestuff is a plant pigment, known as chlorophyll, which, as its name indicates, is responsible for the green color of leaves and other plants. As will be

shown more clearly later on, chlorophyll is, itself, a complicated organic molecule; and we are, therefore, confronted with the following difficulty: Photosynthesis is the only source of organic matter on earth. On the other hand, photosynthesis itself requires the presence of a dyestuff which, in turn, belongs to the class of organic molecules. Under these circumstances, how could the process of photosynthesis ever have started? The answer is that photosynthesis, as it is known today, had a predecessor which produced organic matter without the help of a dyestuff. This proto-photosynthesis must have occurred when no oxygen was present in the atmosphere and, consequently, the ozone layer was also absent. At that time ultra-violet light could reach the surface of the earth, and the absorption of it by carbon dioxide as well as by water molecules could take place directly so that the help of the dyestuff was not needed. The organic matter formed in this way might again have been slowly destroyed by ultra-violet light, were it not for the fact that the substance, once formed, would be taken up by the water and protected from destruction. This condition is the physical basis for the biologist's opinion that life started in the water.

Returning now to the process of photosynthesis in plants, it will be necessary to consider how the process is quantitatively measured. To do this, we write down in a simple chemical equation that which we said before in words.

$$6CO_2 + 6H_2O + E \rightarrow (CH_2O)_6 + 6O_2 \qquad (1)$$

Thus we have in this equation the assumption that a sugar hexose was made by photosynthesis, which requires reduction of six carbon dioxide molecules. It is not essential that the photochemical end-product be hexose itself, but it is essential that the product have an oxidation state of a sugar like hexose. It can then be calculated from the heat of the combustion (E) of such a sugar how much energy is necessary to reduce one carbon dioxide molecule, and we find that the energy is several times greater than the energy transmitted by one visible light quantum to the dyestuff, chlorophyll. The

uptake of carbon dioxide and the evolution of oxygen can be followed manometrically, with the aid of the so-called Warburg manometer. This method makes use of the difference between the solubility of carbon dioxide and of oxygen in water. Unicellular water plants such as algae are used, for the most part, in such experiments. The plants are suspended in water which may fill half of the vessel, and it is connected to the manometer. The gas phase contains air and an admixture of carbon dioxide. If the carbon dioxide molecules are taken up and oxygen is evolved, the pressure will rise, since oxygen is much less soluble in water than carbon dioxide. Among the other methods of measuring photosynthesis, we may describe the spectroscopic one, wherein the amount of carbon dioxide present in the gas atmosphere is measured by its absorption coefficient for infra-red light of wave length 4 $\mu$.

The gas is circulated about an irradiated plant in a closed system through which a beam of monochromatic light passes. Since the amount of carbon dioxide decreases as photosynthesis proceeds, the time of irradiation and the absorption of the monochromatic light by the $CO_2$ becomes smaller with the time of irradiation. The intensity of the light passing through the absorption chamber is thus a measure of the amount of $CO_2$ present at any moment and is measured with a thermocouple and galvanometer.

Before discussing the results of such measurements I should like to mention reasons why the dyestuff, chlorophyll, is especially fitted to sensitize photosynthesis. Figure 5 shows the chemical structure of chlorophyll as now established. Although it is not our task to discuss chlorophyll structure in detail, it may be emphasized that the system of conjugated double bonds, which extends throughout the whole structure, is responsible for the color. The term "conjugated double bonds" means that single bonds between carbon atoms alternate with double bonds. If that system is interrupted by either oxidation or reduction of one of the carbon atoms which belongs to the system of conjugated bonds, the color will vanish, producing the so-called leuco-dye. In

the past this fact has been used as evidence that chlorophyll itself cannot enter the chemical reactions of photosynthesis and undergo periodic oxidation and reduction, since the chlorophyll in a photosynthesizing plant is not bleached at

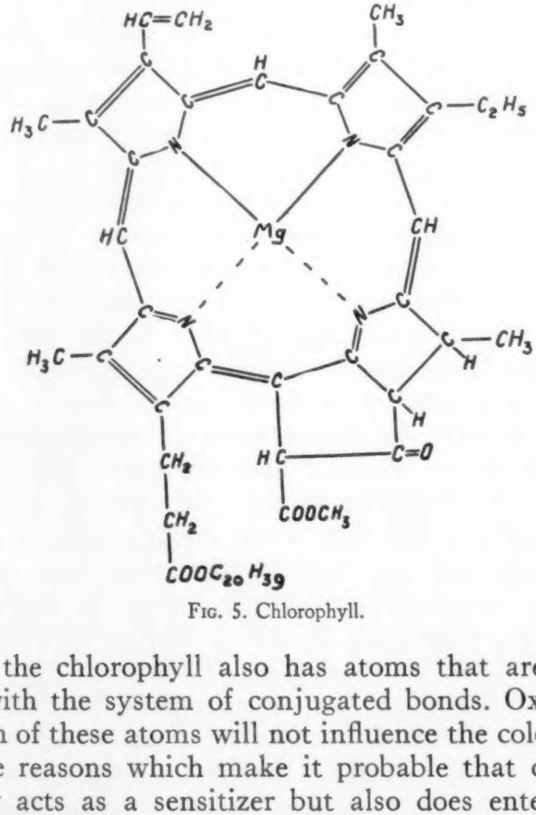



Fig. 5. Chlorophyll.

all. But the chlorophyll also has atoms that are not connected with the system of conjugated bonds. Oxidation or reduction of these atoms will not influence the color. Indeed, there are reasons which make it probable that chlorophyll not only acts as a sensitizer but also does enter into the course of the reaction. But even if it should be demonstrated that chlorophyll is not specific in its chemical reaction, it undoubtedly is specific for photosynthesis by virtue of its physical properties. First, it belongs to the class of fluorescent dyestuffs. The ability of these molecules to fluoresce is always associated with the ability to induce photochemical reactions. Fluorescence means that a part of the light absorbed is quickly re-emitted with or without change of color. This phenomenon is, I suppose, generally well known. I may remind you of the fluorescence of fluoresceine solutions.

Of course, light re-emitted as fluorescence is lost for the purposes of photochemistry and, conversely, if most of the light is used for photochemical processes, fluorescence should be weak. Nevertheless, the fact that a dyestuff is able to fluoresce is important for the photochemical action, since it offers a proof that the energy absorbed remains for awhile as a unit in the molecule and is not dissipated immediately into the degrees of freedom associated with heat movement. Actually, the time during which the energy remains together in the molecule can be calculated from the strength of absorption and the amount of light re-emitted. In the case of chlorophyll, under the conditions prevailing in a plant, the energy stays together for a very short time ($10^{-10}$ seconds), although even this time is long compared to the time of normal kinetic gas-collisions. Due to the fact that the energy is not immediately dissipated, conditions are favorable for it to be transferred to the carbon dioxide and water molecules. In order for this transfer to become effective, the atoms must all be oriented favorably with respect to each other. Since the molecules rotate and oscillate, it may take some time before the right steric configuration is reached. If the energy did not stay together, the right geometric arrangement would have to be present at the very moment of absorption. Inasmuch as this is highly improbable, the photochemical yield is small if non-fluorescing dyes are used as sensitizers. But the ability to fluoresce is shared by chlorophyll with many other dyestuffs. The specificity of the chlorophyll is seen in the fact that it retains only a given amount of energy from the light quanta absorbed, regardless of the color of the light absorbed; the remainder is immediately transferred into heat. That is, the fluorescent light always has the same red color regardless of whether the chlorophyll is irradiated with red, blue, or ultra-violet light. The energy corresponding to a quantum of red light is the amount retained in the chlorophyll and used in the process of photosynthesis. In this way the amount of energy used for the photochemical process is always the same, regardless of the wave lengths of the light absorbed by the chlorophyll. Other-

wise, one would expect that the blue light, which has quanta that are almost twice as great as the quanta of red light, would induce quite different reactions from those of the quanta of the longer wave lengths.

As Figure 6 shows, the absorption is strong in the red and in the blue, whereas in the green region of the spectrum the

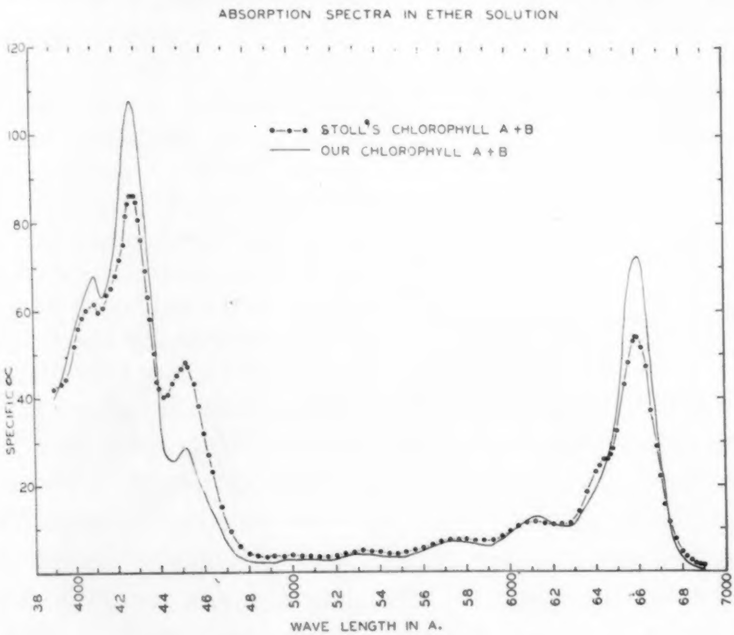



FIG. 6. Absorption spectrum of chlorophyll.

absorption coefficient is small but still not zero, so that light of all wave lengths, throughout the visible region, can be used for the process of photosynthesis. Quantitative measurements of the oxygen evolution or the carbon dioxide uptake and of the energy of the light absorbed make it possible to calculate the number of absorption acts necessary for the reduction of a single carbon dioxide molecule. The value E of the chemical equation (1) allows us to predict that at least four absorption acts would be necessary, since the energy of a quantum of red light is less than one-third the heat of combustion. But the fact that several absorption acts are

necessary leads to the conclusion that the energy absorbed in the form of light energy has to be greater than the amount (E) of equation (1). Each absorption act has to produce an intermediate product of photosynthesis (a partially reduced molecule of carbon dioxide), and the intermediates have to be so stable that they can wait until the next absorption act transforms the product one step further.

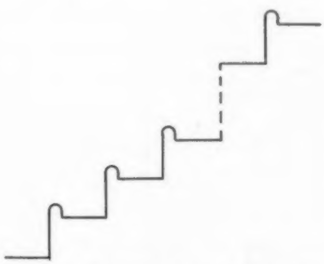


FIG. 7. Energy levels of the intermediate products of photosynthesis.

An extra amount of energy is needed to prevent immediate back reactions of the intermediates to the oxidation state of carbon dioxide. Figure 7 represents an energy diagram similar to that used before in Figure 3. The ground state corresponds to the oxidation state of carbon dioxide. By the absorption of light quanta the first intermediate is formed which, in the diagram, is indicated by a line higher than the one representing the ground state. The two levels are separated by a potential barrier which prevents rapid back reactions. The next light quantum absorbed lifts the molecule one step higher; again a potential barrier has to be overcome and so, after several steps, the level corresponding to sugar and free oxygen is finally reached. To get the necessary stability, the height of the potential barriers has to be so great that it is very unlikely that only four quanta would be necessary to reduce a carbon dioxide molecule, as the earlier measurements of Warburg seemed to indicate. Recent measurements, made in several laboratories, show that ten to twelve quanta are used up in the reduction of one carbon dioxide molecule. Taking into account the fact that some energy losses may occur, for instance, by inefficiency of the chlorophyll, one certainly has the right to conclude that at least eight photochemical steps are necessary and, correspondingly, there will exist at least seven intermediate prod-

ucts between the stage represented by carbon dioxide and water and that of carbohydrate and free oxygen.

The research discussed so far seems to show that photosynthesis is a complicated, sensitized, photochemical process taking place in successive stages, but it reveals nothing which would distinguish photosynthesis in any way from other photochemical processes. However, new assumptions have to be introduced the moment we wish to understand the shape of the curve obtained when the rate of photosynthesis is plotted against light intensity. As shown in Figure 8, photosyn-

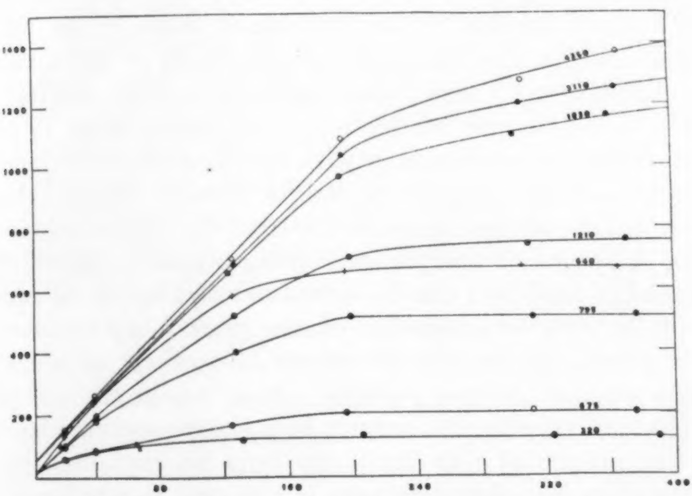


FIG. 8. Rate of photosynthesis as a function of light intensity at various $CO_2$ concentrations (Hoover, Johnston, and Brackett).

thesis at low light intensities is proportional to the strength of the incident light; at medium intensities it rises less rapidly; and at high light intensities becomes independent of further increases in light intensity. In other words, one gets a saturation curve. The rate of photosynthesis at saturation depends upon the amount of carbon dioxide present, but this is true only until a certain minimum concentration of carbon dioxide is reached, which corresponds to a few tenths of one per cent of this gas. A further increase of the concentration of carbon dioxide does not change the situation fur-

ther; in other words, carbon dioxide ceases to be limiting at these concentrations.

Photosynthesis is very efficient in the use of the carbon dioxide present in our atmosphere. In normal air the concentration of carbon dioxide is only 0.04 per cent. At this low concentration the saturation rate is only slightly lower than the maximum rate of photosynthesis occurring in the presence of a surplus of $CO_2$. Indeed, photosynthesis is so efficient that the total amount of carbon dioxide present in our atmosphere is consumed by all the plants on the earth in a very few years. The fact that the concentration in the air remains constant is not a contradiction to this statement, because the amount of carbon dioxide consumed by the plants is given back to the atmosphere by slowly disintegrating organic matter.

The fact that the production of organic matter in plants does not increase constantly with the increase in the intensity of light and the amount of carbon dioxide present above a given limit is of great importance from the biological point of view. A plant is a complicated living organism in which the amount of food that can be stored or used has to be adapted to the other characteristics of the plant; for instance, its metabolism, its growth factor, etc. But there is no purely photochemical process possible which would set a limiting maximum value for this output. In fact, one soon realizes that the occurrence of this limit can only be explained by the assumption that photosynthesis is a process in which not only photochemical processes but also non-photochemical reactions must occur. A total reaction will not proceed more rapidly than its slowest partial reaction, just as a marching troop will travel no faster than the slowest soldier in the group. The velocity of the photochemical partial reactions will, of course, rise proportionately to the intensity of the incident light, but the thermochemical partial reactions necessary to complete photosynthesis are not influenced by light; and one of them will, therefore, at a sufficiently high light intensity, become the slowest partial reaction. At saturation the limited velocity of the slowest dark reaction is alone responsible for the limitation of the output. With this assumption it is possible to calculate from the shape of the

saturation curve the velocity with which the dark reaction has to proceed.

Simple mathematical equations show that at an output corresponding to half the saturation value the velocity of the slowest dark reaction is equal to that of the overall photochemical reaction. This last can be calculated from the quantum yield, the number of chlorophyll molecules present, etc. One gets the result that the slowest dark reaction should run half way to completion in about a minute. On the other hand, it is possible to measure directly the velocity of the dark reaction and to compare this result with the theoretical one. The best measurements of this kind were made by Emerson and Arnold, who used the method of flash illumination. They illuminated plants with brief light flashes and varied the time intervals between the flashes. In Figure 9 the time is plotted as the abscissa and the intensity of the light as the ordinate. Each light flash, then, corresponds to a very narrow column in this figure, while the dark pauses between the flashes are represented by the distances between these columns. If a light flash produces a given amount of photochemical products, the next light flash will find the photochemical apparatus in the same state as did the first, provided the time interval between the flashes is long enough for the dark reaction to run through to its completion. If, on the other hand, the time interval is too short, the subsequent light flashes will find material still accumulated from the previous light flashes, and the yield per flash will, therefore, be smaller than would otherwise be the case. Emerson and Arnold measured the yield per flash as a function of the dark time and, in that way, observed directly the time taken by the slowest dark reaction to run to completion. The result was an unexpected one: the time needed was only about one-hundredth of a second in-

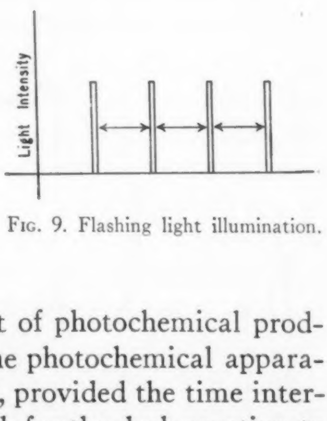



FIG. 9. Flashing light illumination.

stead of sixty seconds. The observation differed from the expectation by a factor of about six thousand. Many attempts were made to overcome this difficulty, but in the present discussion it will be possible to mention only the explanation which we have reason to believe is the correct one.

Calculation of the velocity of the dark reaction is tacitly based on the assumption that all material produced photochemically must undergo a chemical change in the dark before the next photochemical step can proceed. But this assumption is not necessary. One can substitute for this assumption the hypothesis that the freshly formed photochemical products are very unstable; at high light intensities, only a part of the products will then be transformed by a catalytic dark reaction to a new product, which will then be promoted to the next reduction state by light, whereas the bulk of the substance not immediately caught by the catalyst will fall back to the old oxidation state on account of the instability of the newly formed photochemical product which has not undergone the catalytic reaction. Figure 10 illustrates the assumption. The light quanta may transform the $CO_2$ molecule into one with a lower oxidation state, which is protected against back reactions by a very small potential barrier. The lifetime of this freshly formed product is short: not longer than about a thousandth of a second. From the level of the unstable photochemical product a narrow passageway leads down to a much more stable level: that of the catalytically transformed intermediate product. The bottleneck, which

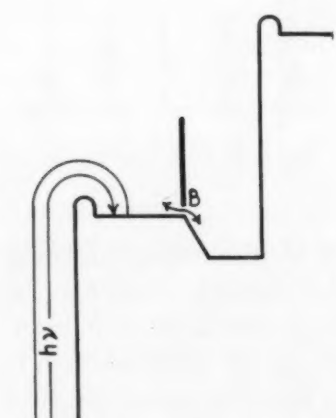



FIG. 10. Schematic representation to show that only a little of the material raised to the higher energy level can get through the narrow passageway (by means of catalyst B) and so reach a more stable configuration. The rest falls back again to the original low energy value.

allows only a certain amount of material to go through the passage, is due to the presence of only a limited amount of the catalyst (designated by the letter B in the figure) which transforms the unstable product into the more stable one. The molecules of catalyst B present can handle only a given amount of material, since it takes some time for each catalyst molecule to go through the reaction cycle. All of the photo-product that the catalyst B cannot handle will not accumulate in the unstable state, but will fall down in the lower state, as indicated by the arrows. It is necessary to assume that catalyst B has to act on each photochemical intermediate product of photosynthesis; in other words, all the freshly formed photo-products are supposed to be unstable and have to be stabilized by a catalytic reaction involving B. This follows from the fact that, under normal conditions, the relative concentrations of the intermediates are the same at saturation and at low light intensities. Otherwise, one would obtain a temporary anomalous rate in weak light immediately after an exposure to a strong irradiation. The time measured in Emerson and Arnold's experiments is, then, the time necessary for a catalyst B molecule to go through a reaction cycle, and the maximum yield per light flash is the measure of the number of catalyst molecules present. This hypothesis explains satisfactorily the occurrence of the saturation and the result of the flash experiments mentioned.

The foregoing hypothesis can be tested by experiments on fluorescence of green plants (Franck, French, and Puck). It was mentioned in the introduction that, when most of the energy is used for photochemical processes, the fluorescence, *i.e.*, the re-emission of light, is necessarily weak. If, on the other hand, a part of the chlorophyll is connected with material which is not able to take up the light energy for chemical processes, the fluorescence will be stronger. Indeed, this can be shown in living plants when, by addition of narcotics, the surface of chlorophyll is covered with photo-insensitive material (Wassink, Vermeulen, and co-workers). These substances hinder the flow of energy from the chlorophyll to carbon dioxide and intermediates and, therefore, reduce the

photosynthetic output and at the same time raise the strength of the fluorescent light. Measurements of the intensity of the fluorescence will, consequently, show whether the limitation of photosynthesis is accompanied by an accumulation of photo-insensitive material in contact with the chlorophyll or whether the limitation occurs in such a way that no accumulation of photo-insensitive material takes place.

It is clear that the hypothesis put forward above emphasizes the statement that no photo-insensitive material will be accumulated, since it is assumed that the saturation is caused by the limitation of a catalytic reaction acting on a chemically unstable product. The product formed by the aid of catalyst B is photo-sensitive, as is the substance resulting from the rapid back reactions. The concentration of the unstable photo-product, which may be photo-insensitive, always remains exceedingly small. Indeed, measurements of fluorescence show that the fluorescence intensity rises in a linear ratio with light intensity in an intensity region that is already producing saturation of photosynthesis. If normal saturation were associated with an accumulation of photo-insensitive material, the fluorescence should rise faster than linearly in the intensity region where the photosynthesis curve shows the transition to saturation.

The dark reaction involving catalyst B is not the only one associated with photosynthesis. This can again be shown by experiments on saturation in continuous and flashing light, by fluorescence experiments, and by important results gained by Kamen, Ruben, and co-workers who used the method of labelled carbon atoms.

The saturation rate of photosynthesis is very sensitive to cyanide. The question arises whether cyanide poisons catalyst B or whether some other catalyst, which is present in a surplus under normal conditions and so has no effect on the saturation rate, is so much reduced in its activity by that poison that it becomes limiting. If the number of active B molecules would be reduced by cyanide, the maximal photosynthetic gas exchange obtainable by single light flashes

should also be reduced. Actually this yield remains unaltered by the addition of HCN. But the duration of the dark periods between two consecutive flashes necessary to attain this maximum yield per flash becomes prolonged by the addition of the poison. Just this behavior is to be expected if the dark period is, in the presence of cyanide, not only a measure of the time needed by catalyst B to go through its reaction cycle, but is also influenced by the limitations of a second catalytic reaction.

The cooperation of the two catalysts, B and A, not only changes the duration of the dark period, but also alters the shape of the curve showing the yield per flash *versus* dark period, in a characteristic way. This may be seen in Figure 11,

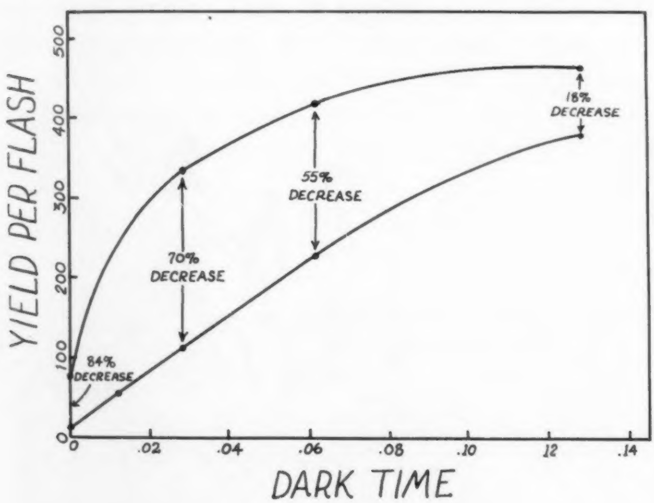



Fig. 11.

where a curve without cyanide is presented above one measured in the presence of that poison. It will not be possible to give a detailed discussion of the consequences to be drawn from such measurements but only to mention that catalyst A works on a stable substrate. One must, therefore, expect that the fluorescence rises more rapidly than linearly as saturation in the presence of cyanide is approached; that is,

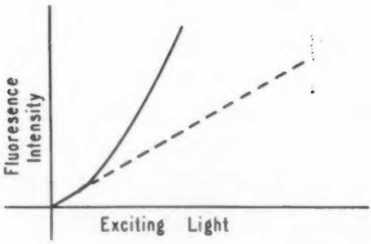



Fig. 12. Fluorescence as a function of light intensity in a cyanide-poisoned leaf (Wassink and Katz, and Franck, French, and Puck).

in opposition to the behavior at normal saturation. Figure 12 shows that the fluorescence plotted as the function of light intensity shows the expected deviation from linearity.[1] It was also possible to discover the function of catalyst A. According to the work of Kamen and Ruben, who made use of the radioactive tracer technique, carbon dioxide reacts in the dark with an acceptor molecule. This reaction is assisted by a catalyst sensitive towards cyanide. The compound formed by the acceptor molecule and carbon dioxide constitutes the photosensitive substrate.

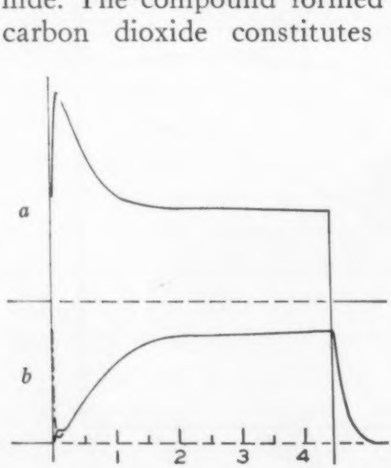



Fig. 13. Course of fluorescence.

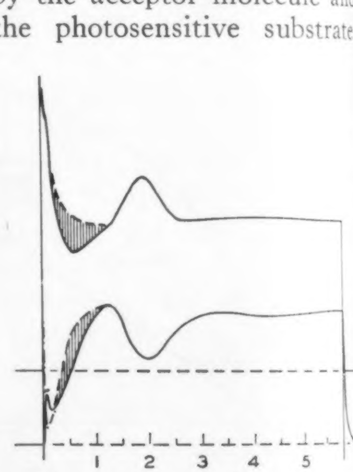



Fig. 14. Fluorescence and photosynthetic output.

Lack of $CO_2$ has the same influence on the saturation and fluorescence curves as does cyanide in the presence of a surplus of $CO_2$. In both instances the amount of substrate which undergoes the photochemical reduction process is deficient.

[1] A deviation from linearity occurs also without cyanide and in the presence of enough $CO_2$, but in this case only at very high light intensities and in some plants at intensities much greater than is required to obtain saturation. This effect is produced by a secondary process not to be discussed here.

We must mention a third catalyst, the influence of which on the rate of photosynthesis can only be observed at the beginning of an illumination period. Again it is a catalyst that acts on a substrate stable enough to be accumulated if the catalyst (called catalyst C) is limiting. The time course of the rate of photosynthesis and of the fluorescence intensity consequently run antiparallel (work of McAllister and Myers). A few examples may show this. Curve *a* of Figure 13 shows the time course of the fluorescence in a higher plant, to be compared with curve *b*, the time course of the rate. There is a strong maximum of the fluorescence after one second of illumination, to which corresponds the deep minimum of the photosynthetic rate. Figure 14 shows a more complicated set of curves, shown here to prove that each fluctuation of fluorescence is mirrored in the anomalies of the photosynthetic output.

Figure 15 shows that the duration of the fluorescence outburst is prolonged by an excess of $CO_2$ (the same is true

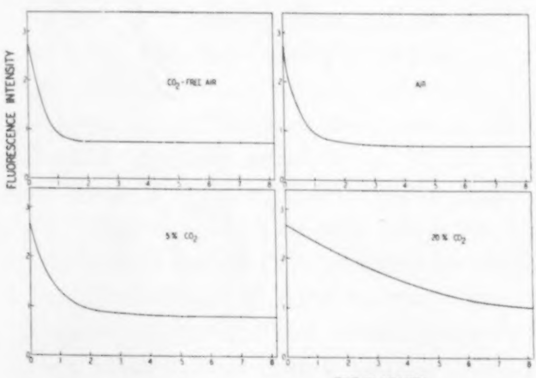



FIG. 15. Effect of $CO_2$ in prolonging the time of the fluorescence decay.

for the induction period of photosynthesis); with 20 per cent $CO_2$ it lasts, for instance, about 20 minutes, compared with about one minute in normal air. This fact can be used for a demonstration of the velocity with which a gas exchange takes place in a leaf. To do this, the surface of a leaf, provided with an atmosphere containing a small amount of carbon dioxide, is exposed to a strong illumination so that

the fluorescence outburst fades away in about a minute. A small portion of the leaf, however, is connected to a rubber tube through which gas containing a high concentration of carbon dioxide can be admitted. This part of the leaf will then be exposed to an excess of carbon dioxide, and the fluorescence will, therefore, remain strong for several minutes in that part of the leaf. At one minute after the beginning of irradiation the part of the leaf containing the excess of carbon dioxide fluoresces much more strongly than the other parts of the leaf. The spot which is brighter than the surroundings is not confined to the part directly connected with the rubber tube, since the carbon dioxide diffuses from this spot to other parts of the leaf. One can thus actually photograph this diffusion of the carbon dioxide through the leaf with the fluorescent method.

It will not be possible to discuss the details of the anomalies shown in Figures 13 and 14, but I may state that they are readily understandable. The function of catalyst C is to split off oxygen from the peroxides formed as one of the photochemical end-products of photosynthesis. The concentration of catalyst C molecules is sufficient to prevent any limitation of the rate of the reaction in which it is involved if all the molecules are in an active form. But the ratio between the number of active molecules of catalyst C to its inactive fraction depends upon the rate of photosynthesis. Catalyst C is slowly deactivated (apparently) by an oxidation process and reactivated by a reaction with the carbohydrates. Whenever the rate of photosynthesis is suddenly increased, there is a transition period during which C is limiting until enough molecules are activated. The anomalies mentioned are a direct consequence of this temporary insufficiency of the peroxide-splitting catalyst. The induction period can become of great importance for the total growth of the plant provided the plant is periodically illuminated and darkened. The deactivation of the catalyst C in the dark takes about a minute and the reactivation about the same time. The plant is, therefore, practically prevented from growing if the periods of light and dark are approximately a minute in duration.

The connection of this phenomenon with the induction period was first recognized by McAllister.

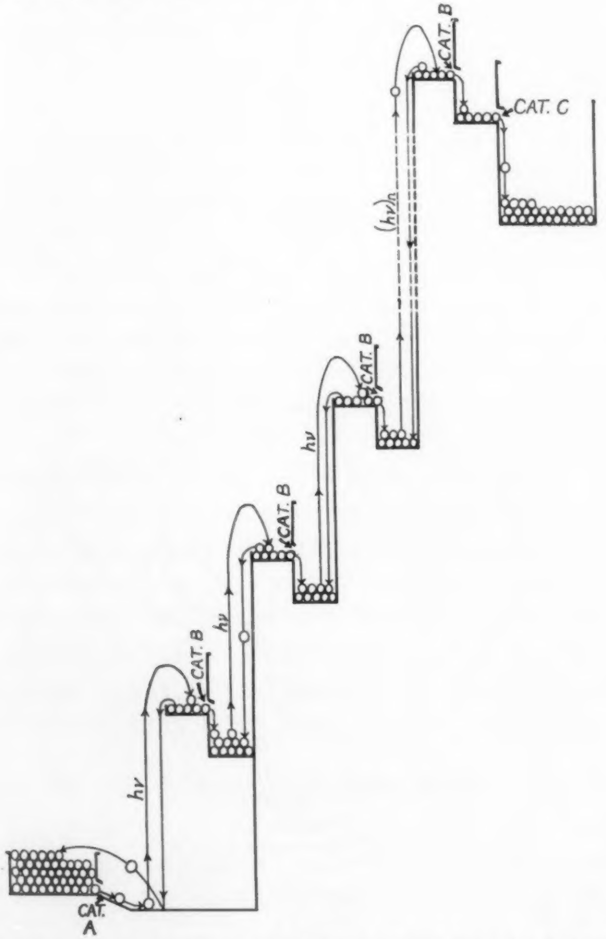



FIG. 16. Schematic representation of the course of the photochemical and catalytic reactions of photosynthesis.

Figure 16 summarizes in an energy diagram the results of the cooperation between photochemical reactions and catalytic dark reactions. The reactions must proceed with the help of photochemical steps from the low level of the carbon dioxide and water to the level of the carbohydrates and free oxygen. The first step is an exothermic reaction

between carbon dioxide and the acceptor molecule, which takes place with the help of the catalyst A. That this reaction has limited capacity is indicated by the narrow opening between the level of carbon dioxide and free acceptor molecules and the level of the carboxylated product. From this lowest level on, light quanta will raise the molecules in successive steps to the highest level, which corresponds to that of carbohydrates and peroxides. After each photochemical step, there is a narrow gateway leading from the unstable photochemical products to the stable ones. The unstable ones are protected only by a small potential barrier, so that all the material that cannot pass quickly enough through the bottleneck formed by the catalytic reaction involving catalyst B will undergo back reactions. At the highest level there is again a catalytic reaction, that serves to split off the oxygen from the peroxides.

Let us, finally, introduce a few chemical equations, which may serve at least to illustrate the kind of chemical reactions that may be expected to occur. The preparatory dark reaction is written down as a carboxylation reaction. The substance RH may, itself, be a carbohydrate if we accept the assumptions of Kamen and Ruben. Then there follow eight photochemical steps. We assume here that they belong to two groups, one group in which, with the help of the light energy

$$RH{\cdot}CO_2 \xrightarrow{\text{Catalyst A}} RCOOH$$

| | | | | | | |
|---|---|---|---|---|---|---|
| 1. RCOOH | + H Chph* | + hν | $\xrightarrow{\text{Catalyst B}}$ | Intermediate | I | + Chph |
| 2. Intermediate I | " | " | " | " | II | " |
| 3. Intermediate II | " | " | " | " | III | " |
| 4. Intermediate III | " | " | " | $(CH_2O)_6$ + Chph | | |

| | | | | | |
|---|---|---|---|---|---|
| 5. Chph | + ROH | + hν | $\xrightarrow{\text{Catalyst B}}$ | H Chph | + RO |
| 6. " | " | " | " | " | " |
| 7. " | " | " | " | " | " |
| 8. " | " | " | " | " | " |

9. $2RO \rightarrow ROOR$

$$ROOR + H_2O \rightarrow + ROOH$$

$$2ROOH \xrightarrow{\text{Catalyst C}} ROH + O_2$$

* Symbol for non-dehydrogenated chlorophyll.

absorbed by the chlorophyll, hydrogen atoms are transferred from the chlorophyll itself to the substance RCOOH, reducing it to a carbohydrate, while the four chlorophyll molecules are each deprived of one hydrogen atom. The mono-dehydro chlorophylls produced in this way must regain the hydrogen in order to be able to act again as hydrogen donors. It is assumed that this is done also with the help of a catalyst that takes away the hydrogen from an organic molecule ROH, transforming this substance into radicals which, by addition of water, form an organic peroxide. The peroxide may be attacked by catalyst C, which splits off oxygen and reproduces ROH.

It should be emphasized that this chemical picture serves only as an illustration. Future chemical experiments will certainly change the picture considerably, but one can hope that the main interaction between photochemical and catalytic reactions is correctly interpreted by the theory outlined above.

## National Sigma Xi Lectureships for 1942

THE FOLLOWING lectures have been chosen for the 1942 National Lectureships. Detailed information was sent to the chapter secretaries during April. Requests from chapters are to be received by November 1.

H. A. Bethe, Cornell University—"Stellar Energy"—March 15-April 15.

P. W. Bridgman, Harvard University—"Some Recent Work in the Field of High Pressures"—February 15-March 15.

H. M. Evans, University of California—"Hormones of the Anterior Hypophysis"—April-May.

J. G. Kirkwood, University of Chicago—"The Structure of Liquids"—March.

L. S. Marks, Harvard University—"Modern Power Generation"—April.

# THE SOCIAL IMPLICATIONS OF RESEARCH[1]

By James R. Angell
New Haven

DISTORTED and narrow views about the nature and function of research are curiously prevalent and to no small extent in college circles. It has occurred to me that I might with propriety improve the present opportunity by pointing out some of the deep underlying social aspects of research which many ill-informed persons are apt to regard as a needless luxury, but which is in point of fact in the modern world an indispensable necessity. Actually, research represents one of the most essential functions of organized society, and no social order could long maintain itself in which it did not occupy a strategic position. Often associated in the minds of the ignorant with eccentricity and a somewhat arid and juiceless temperament, it is in reality a reflection of exactly those traits which inspire the explorer, which lead to discovery in every realm of thought, and which are concerned with the incessant revision of previous knowledge in terms of the constant growth which such knowledge undergoes. From the point of view of the person conducting it, much research is characterized by the essential qualities of the artist. It springs from very deep impulses in human nature and leads on to consequences of fundamental social import.

The main agencies under which research is conducted in the United States may perhaps be grouped under the following five headings, although this is in no sense an exhaustive classification. Moreover, the groups overlap to a certain extent. It is, however, suggestive and will enable me to discuss briefly the several distinguishable features of our national organization in this field with more brevity and clarity than if these differentiations be disregarded.

1. National Academy of Sciences and the National Research Council.
2. Research Institutes.
3. Industrial Laboratories.
4. The National and State Experiment Stations and Research Divisions.
5. Universities.

[1] Based upon an address to the Yale Chapter April, 1941.

I shall take these up in order and comment briefly upon each.

1. In England and on the Continent the Royal Societies and Academies enjoyed relatively unrivalled prestige in the field of scientific research until a comparatively recent period. They were somewhat in the nature of aristocratic clubs devoted to the encouragement of scholarly and scientific activities, exercising their influence largely through their official sessions before which were read the papers of their members and occasionally their guests. Many of them began early to print these papers in the form of Proceedings and a considerable portion of the most significant scientific contribution of the last century or two first came to public attention through such publication. Some of these organizations presently acquired modest resources which they could at their discretion employ to foster or subsidize particular types of research.

In the United States, the National Academy and its child, the National Research Council, have exercised a very stimulating effect upon fundamental research and they have from time to time been given funds which they have employed to encourage outstanding research activities.

When Cardinal Newman was writing his essays on "The Idea of the University" he reflected a then relatively common attitude in England that academies should be the principal agents in the responsibility for scientific research, the universities being on this view quite definitely exonerated from such obligations. Needless to say, this conception was quite at variance with that current in Germany and, in general, among continental universities, and it has now been discarded almost everywhere. In any case, the academies and learned societies serve now rather to stimulate and pass upon the value of research, than to carry on such research as an intrinsic activity of the organization.

2. Research Institutes have developed in the United States in the last three decades with remarkable rapidity and there is almost no field of human endeavor in which examples are not to be found. While I have not undertaken a census, my impression is that more of them have been in the field of medicine and the biological sciences than in any other one area, but chemistry, physics, in a sense mathematics, as well as economics and certain of the social sciences are all represented. Though they do not belong definitely in this group, many of the larger museums could well be included here because they produce research of the highest quality covering a very wide area of scientific activity. Unlike the institutes, however, members of a museum staff, even when primarily engaged upon research, ordinarily have other duties which absorb a portion of their time and energy.

The Research Institute has as its great characteristic the presence of a group of highly trained scientists who give their entire time to research activities, including publication. This means that the men in an institute staff are in the first instance a carefully selected group; that they are able to plan their line of march for a considerable time in advance; that they have practically no other obligations, and it may be added that in most instances they are provided with comfortable salaries which leave them measurably free from serious anxiety. Much of the very best work which has been done scientifically in the last generation has come from these institutes. They constitute most attractive outlets for research activity of high quality and their return to the society which supports them has justified their existence many times over. If space permitted, one could give innumerable illustrations to prove this last statement.

3. The Industrial Laboratory, as originally conceived and developed, was concerned primarily with the promotion of the particular product flowing from a special factory. It was in part concerned with standardizing procedures and in part with the devising of new and improved techniques relevant to the industrial processes in the concern supporting it. But within the last few decades this picture has changed radically and in the laboratories of many of the larger commercial and industrial enterprises the research scientist has been given the widest scope and permitted to carry on investigations quite regardless of their immediate promise of financial returns to the company in question. Furthermore, not a few of these organizations with sound imagination and no little courage have invested very large sums of money in the support of such research and, partly by reason of the large salaries paid and partly because of the remarkable opportunity offered, they have been able to attract into their service many of the most distinguished scientists of the day.

The upshot of all this development has been the opening up of a new and extremely attractive career to scientific men of the highest quality and out of these laboratories, in addition to the contributions to applied science, has issued an extraordinary body of the very finest research in the field of pure science, that is, research carried on with no specific reference to practical applications.

4. The national government and the various states in the Union have developed research on a very large scale, much of it relating to one or another of the branches of agriculture. Nevertheless, it would be difficult to mention any scientific field in which some government agency is not active. The geological surveys of the federal and state governments date back to quite an early period and they have been of extra-

ordinary value in disclosing the resources of the country. The geodetic surveys have been of very great value in the execution of topographic measurements and in the making of maps. As in other instances, such research has constantly contributed to the improvement of the methods employed, so that the results are more accurate and often more speedily and less expensively attained. The investigations of our great forests, the studies of the various diseases and enemies which afflict our trees, and for that matter plant life of every kind, are constantly being carried forward with the most valuable results in the preservation and development of these parts of our national wealth. The Department of Mines, in conjunction with the Geological Survey, has explored every angle of our mineral wealth and the methods of exploiting it for the public good. The Bureau of Fisheries is constantly studying the life history of our fishes and devising means for their protection and propagation, again to the great national advantage. The Meteorological Service is incessantly studying the problems of weather prediction and, both for agriculture and for shipping, its services have become entirely indispensable.

Broadly speaking, I think it may be said that every department of the Federal Government is constantly engaged in researches designed to render its services more valuable and in this respect the States have been active imitators, although the range of their researches is not in the case of any single State comparable with those of the Federal Government, with which in most instances they cooperate effectively. The Army and the Navy are both active contributors to research, especially in the broad field of engineering, including aviation, and in the nature of the case these departments, like a number of others, are deeply concerned with standardizing and testing processes.

When all these branches of government activity are brought together, there is presented a quite overwhelming picture of the magnitude of the research enterprises thus going forward. Many thousands of men are involved, and in every case they must be men of sound professional training and with marked natural gifts for the work of investigation.

5. This brings us to the last of the groups that we undertook to distinguish from one another, i.e., the Universities. They figure in the picture in two highly important ways: First, as the intrinsic source from which a very large part of the most disinterested scientific research emanates. Inevitably and properly, there is in a university a certain amount of research carried on which is directed to more or less practical aims. This is especially true of the engineering, the agricultural, and the medical departments in universities, but on the other hand far the larger part is instigated by motives of sheer intellectual interest

and curiosity. Be it said the line of demarcation between pure and applied science is anything but sharp and distinct, and the same thing is true of the differences between research in these two divisions of scientific activity. Second, and as an essential outcome of the first function, the universities are the great training grounds for expert research workers. There is no other considerable source from which such trained personnel is to be derived. Obviously, the only satisfactory method of selection for research talent and the only reliable means of training it is that practiced by the universities, where the native talents of men for work of this kind can be tested and where, when found, such talents can be disciplined.

It is a somewhat extraordinary circumstance, in view of these two indispensable functions of a university in the area of research, that it should have taken so long to establish the position of research in American universities. It is little more than half a century ago since the importance of research as an essential element in the modern university began to gain general acceptance in our country. There had, of course, been outstanding examples of individual investigators in American faculties, many of whom had achieved notable distinction as creative scholars and scientists; but it did not follow from this that the universities themselves made adequate provision for students who desired to carry on research.

It is even now in many of our universities, in which the Arts College still conceives itself as the center of the universe, a common subject of student newspaper editorials in which the critical importance of teaching, as contrasted with research, is played up and in which the research worker is pictured as a "dry as dust," totally unfitted to teach undergraduates.

Editorials of this character reflect in part the profound ignorance of their writers of the status of research in the modern world of intellect. They reflect also very often the instigation of faculty members who either have no qualifications for creative scholarship, or who happen to be working in fields in which research is relatively difficult and unrewarding. Moreover, there can be no question at all that some extremely brilliant investigators have neither interest in, nor talent for, teaching undergraduates—especially in the elementary phases of subject matter. And it is a lamentable fact that our collegiate curriculum still has in it a considerable body of rudimentary material of essentially secondary character.

On the other hand, no one can long continue to be a really stimulating and valuable teacher of undergraduates, no matter how many amusing classroom tricks he may display, who does not possess an essentially

inquiring mind and who is not constantly engaged in the effort to extend his command over his field and, if possible, to add to the available knowledge involved in it.

Unhappily, the test of such qualities is often identical with publication and, as a by-product of this emphasis, no small amount of unimportant and second-rate material gets into print. Nevertheless, the university teacher who over the years is never willing through publication to expose his thinking and study to the critical comments of his scholarly peers, may justly be regarded as subject to some suspicion. Certain of these teachers exploit a fictitious perfectionism, maintaining that they are not willing to publish until they have completely satisfied themselves that their work cannot be further improved, with the result that often their careers come to a close with nothing to show for them in the form of the printed page. Others allege, in season and out, that their obligations as teachers leave them no time for any constructive work—and this in the face of the fact that almost all teachers enjoy a considerable summer vacation in which activities of this kind can be pursued, if the disposition and the ability so to do is at hand.

All this commentary on the university adds up to the fact that in subserving the great social function which belongs to research the universities are absolutely indispensable elements and this, not only because they set the highest standard of disinterested research in all fields of intellectual exploration, but also because they are the only great reservoirs from which the other research agencies can hope to draw their personnel.

I trust that this statement, brief and incomplete as it is, may reasonably have served the two purposes I had in mind:

First, to make clear the highly important social function represented by research, together with the truly impressive dimensions it has assumed in the United States; and

Second, to convey to young students the exciting and intriguing potentialities of research as a career. For men and women who possess the necessary mental and moral qualifications (and the second are quite as essential as the first) it combines the possibility of valuable contributions to society with the opportunity to follow one's intellectual interests to their uttermost boundaries.

# SOME BIOLOGICAL ASPECTS OF VISION[1]

By S. R. Detwiler

Department of Anatomy, College of Physicians and Surgeons, Columbia University

FOR a quarter of a century a good fraction of my time and energy has been spent in carving the embryos of salamanders. In so far as I am aware, this has not been done to satisfy any sadistic tendencies, but to learn something about the growth of nerves in the embryo. I have had also a sustained interest in the structure-function correlations in the vertebrate retina. Extending over a period of twenty-five years, I have collected the eyes of various vertebrates. These have been studied primarily through the eyes of an anatomist, and it might be well to state that I am neither a physiologist nor a chemist, and hence cannot speak with authority about spectral physiology or the photochemistry of vision, although it may be necessary to refer in an elementary way to certain of these aspects of visual function.

A fact of fundamental importance concerning vision was made in 1866 by Max Schultze, who discovered that the vertebrate retina, and particularly that of man, possesses two types of visual cells, viz., rods and cones, and that these elements subserve different visual functions. The so-called Theory of the Double Retina (Parinaud) or the Duplicity Theory (Von Kries) is based upon the findings of Max Schultze. The Duplicity Theory as it is generally referred to, maintains that the rods are concerned with colorless (scotopic) vision at low intensities of illumination, and that the cones constitute the apparatus concerned with vision at high intensities, as well as with the perception of color. The cones are not regarded as being utterly useless at night, but relatively so, for the majority of them possess thresholds which are much higher than the highest thresholds of the rods.

This theory, since its original conception has been generally regarded as well substantiated, and in recent years it has received support by many physiologists, notably by Hecht (1937, 1938) and his associates in their physiological measurements on dark adaptation, intensity discrimination, visual acuity, and the phenomenon of flicker. Certainly from their results it would seem that the Duplicity Theory need not be referred to as theory but as fact. In the light of this theory, therefore, the presence and relative distribution of rods and cones in the eyes of

[1] Based upon a lecture given before the Alabama Chapter, November, 1940.

vertebrates becomes a matter of first importance to anyone who wishes to study vision from a comparative point of view.

The various layers of the retina and the structural elements composing them are brought out in Figure 1. It is generally assumed that each cone makes a centripetal synaptic connection with a single bipolar cell, whereas several or many rods become related to the dendritic endings of a single bipolar cell (Figure 2). Such a condition presumably provides for summated conduction of the rods and for individual isolated conduction of the cones, thus not only enhancing rod vision at low illuminations, but favoring greater visual acuity of the cones at high illuminations. This supposed structural situation, however, is not borne out by all illustrations.

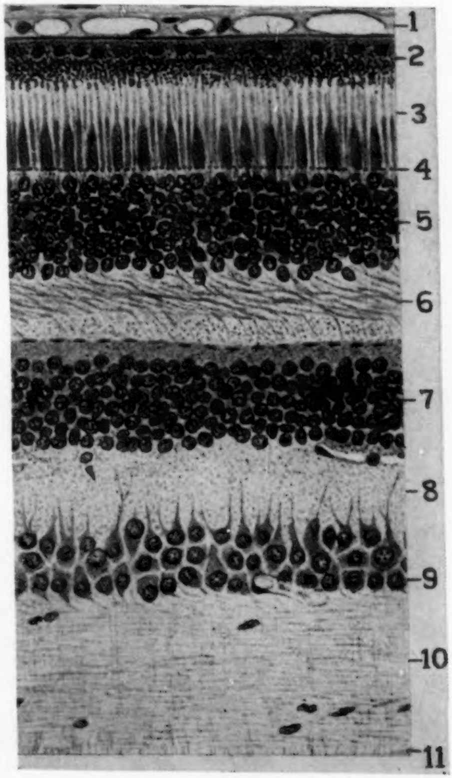



FIG. 1. Section through the human retina (from figure 417, Bailey's Textbook of Histology, 10th Ed., Williams and Wilkins Company, Baltimore, 1940. 1, choroid; 2, pigment epithelium; 3, rods and cones; 4, external limiting membrane; 5, external nuclear layer; 6, external molecular (plexiform) layer; 7, internal nuclear layer; 8, internal molecular (plexiform) layer; 9, ganglion cell layer; 10, nerve fiber layer; 11, internal limiting membrane.

## *Structure of Visual Cells*

One of the chief interests in the morphology of visual cells lies in the great variability which they exhibit in form size and structure. So great is this variation in certain instances that some confusion has arisen at times as to whether certain elements are rods or cones. Mademoiselle Verrier (1935) regards the so-called rods and cones as representing extreme structural variations of a single photoreceptor cell, thus doing away with the concept of morphological and functional duality in the retina. In addition to the physiological evidence, however, which

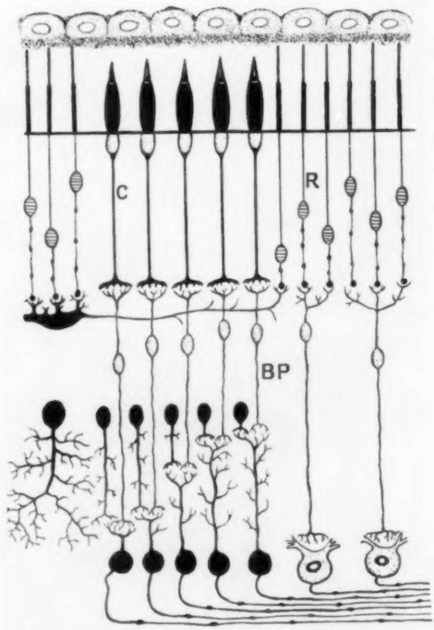



Fig. 2. Plan of the retinal neurones as shown by the Golgi method, showing individual connection of the cones (c) with a single bipolar cell, (BP) and multiple connections of the rods (R) with a single bipolar cell (redrawn from Greef and Cajal).

definitely demands a functional duality in the retina, there are other criteria which, when combined, leave no doubt as to the existence of structural duality as well.

Cones and rods are characterized by the possession of two major portions—an inner and an outer segment. Typically the outer segment of the cone is conical in shape, whereas the rod outer segment is cylindrical. Both elements possess a nucleus which lies on the vitreal side of the external limiting membrane (Figure 1). The cone inner segment contains a myoid element and an ellipsoid. In many forms there is present also a highly refractive globular structure, called the paraboloid. Oil drops are present at the distal end of the inner segments of the cones in amphibians, reptiles (turtles and lizards) and birds (Figure 3). They are absent in teleost fishes, crocodiles, mammals and anthropoids. In the chick retina they are red, golden and greenish yellow, and according to Wald (1939) they form a color filter arrangement much like that employed in many systems of color photography. If the cones of all vertebrates were to possess colored oil drops, the whole problem of color vision might be simplified.

Whereas rods typically possess a myoid and an ellipsoid, there is only one vertebrate form which I have studied that possesses a paraboloid. This is in the nocturnal Gecko (Figure 4D). Oil drops are absent in the rods of vertebrates.

Structural differentiation between rods and cones is usually based upon the form of the outer segment (cone-shape vs. rod-shape). This criterion fails in the region of the macula, where the cones are usually

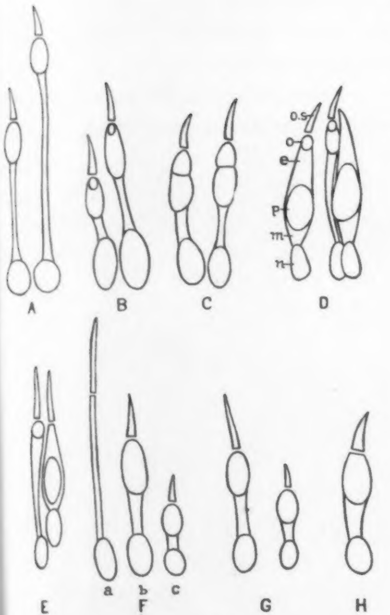



Fig. 3. Cones from various vertebrates. A, catfish; B, frog; C, alligator; D, lizard; E, chicken; F, Marmoset (a, foveal cone, b, parafoveal cone, c, peripheral cone); G, rhesus monkey; H, man. n, nucleus; m, myoid; p, paraboloid; e, ellipsoid; o, oil globule; o.s, outer segment.

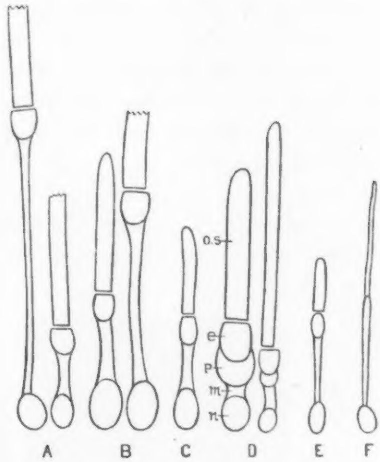



Fig. 4. Rods from various vertebrates. A, catfish; B, frog; C, alligator; D, night lizard (*Gecko*); E, chicken; F, monkey. n, nucleus; m, myoid; p, paraboloid; e, ellipsoid; o.s. outer segment.

long attenuated structures which morphologically look like rods. Regardless of their shape, however, their known function fits in entirely with the physiology of cone vision. Cones are usually regarded as making centripetal dendritic connections with the bipolar cells, whereas rods have molecular ending (Figure 2). Kolmer has shown also a definite difference between rods and cones upon the basis of their staining reactions. Furthermore, in many groups of vertebrates, further identification is rendered possible by the opposite (inverse) phototropic responses to light. The cone myoid shortens in the light and elongates in the dark; the rods exhibit the opposite reactions. It is thus seen that not only do we have physiological evidence which demands the presence of two different populations of visual elements, but there are morphological and other criteria which definitely support the fact that there is a structural duality in the retina.

*Retinal Structure and Animal Habits*

So closely correlated is the mode of life of many animals with the structural make-up of the retina, that I think from an histological

examination of the retina one can predict with reasonable assurance something of the habits of the animal as well as its visual ability.

Whereas the majority of vertebrates possess both types of visual cells, there are notable exceptions. Some forms possess one type only and in such forms their mode of life is correlated with the particular type of photoreceptors which they possess. The majority of reptiles possess pure cone retinae (Figure 5). Some have a double retina (e.g., alligators), and still others have a pure rod retina (e.g., the Gecko, Figure 6). Those reptiles possessing cones only are diurnal in

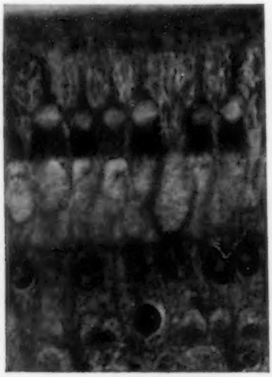


FIG. 5 (*left*). Photomicrograph showing pure cone retina of the turtle. Note large paraboloids and oil globules. × 650.

FIG. 6 (*right*). Photomicrograph showing pure rod retina of the nocturnal lizard (*Gecko*). × 650.

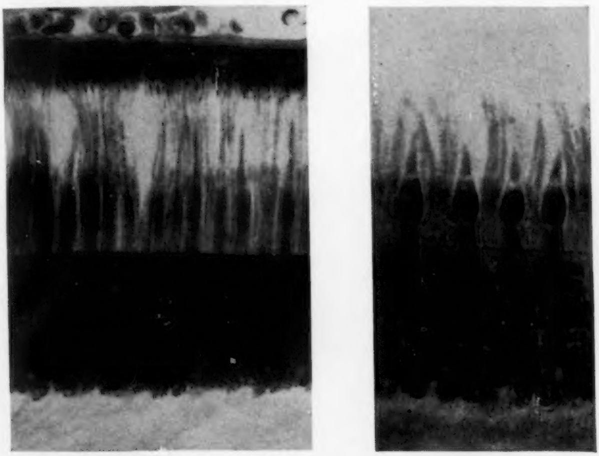
habits, and apparently have little capacity of vision in dim light. On the other hand, such forms as the Gecko which is cone-free, and the crocodile with its rod-rich retina, have a mechanism particularly adapted for nocturnal vision. It has been my personal experience to observe the activities of the Geckos which never begin until dusk.

We are all aware from personal experience that our domestic neighbors, the rats and mice, are much more "on their toes," so to speak, at night than they are in the daytime. Their retinas are made up, almost if not entirely, of rods. The bats, which possess a pure rod retina, begin their activities with approaching dusk.

Upon this same basis of structural differentiation in the retina, birds become divisible into two functional groups, viz., day birds and night birds. We all know that some kinds migrate during the daytime and settle down for the night, whereas others migrate only at night and almost yearly we hear of scores of migrating night birds which encounter

death on the wing, by flying into strongly illuminated tall buildings, apparently dazzled by the bright light.

With the exception of the so-called owl monkey (*Nyctipithecus*), all the monkeys, the great apes, and man possess a double retina (Figure 7). The relative numbers of rods and cones, however, or the rod-



a b

Fig. 7. Photomicrograph showing (*a*) parfoveal rods and cones and (*b*) peripheral rods and cones in the retina of the monkey (*Macaccus rhesus*). × 630.

cone ratio, changes in different parts of the eye. Certain prosimian forms, such as the lemuroids which include the so-called Pottos, Lorises, and Galagos, are typically nocturnal in their habits. These animals leap from bough to bough only at night when they also do their feeding. Figure 8 is a photograph of the slow-moving Loris (*Nycticebus tardigradus*) which has been in captivity under my own observations. This animal was so light-sensitive that photography was difficult. The moment one turned on a lamp of 60 watts, this creature either turned its head away or buried it between its legs. Both Loris and the Galago mala (another lemuroid under my observation) fed only at night. A photomicrograph of their respective retinas is shown in Figure 9. Both retinas possess closely packed filamentous rods and are entirely devoid of cones.

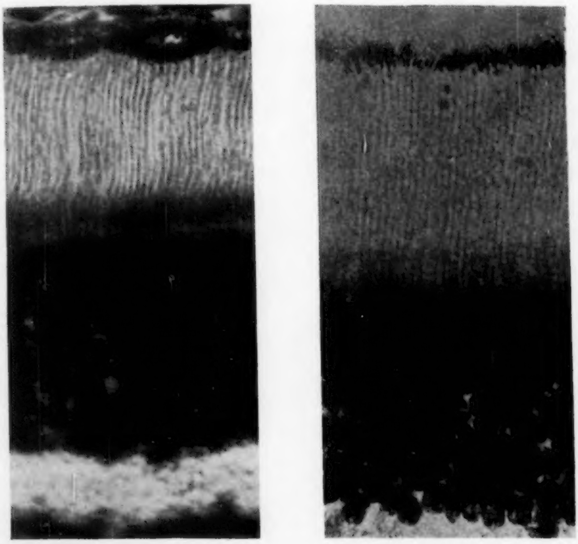
Perhaps the chief interest in these nocturnal animals lies in the structure of the retina, but their eyes exhibit other features that are also characteristic of nocturnal vision. The cornea exhibits a marked curvature and is much larger in relation to the size of the eye as a whole than in the diurnal anthropoids and man. The anteriod chamber and

FIG. 8. Photograph of a living nocturnal lemuroid (*Nycticebus tardigradus*). Note very large cornea and a vertical oval pupil (See figure 10).

lens are also relatively much larger. The contrast is shown in Figures 10 and 11. It is apparent that these nocturnal lemuroids have a much more efficient light collecting and refracting mechanism than do the diurnal anthropoids. *Nyctipithecus,* a true monkey, but of nocturnal habits, has an eye which, in these respects, resembles closely that of the lemuroids rather than that of the other anthropoids. It is clear, therefore, that structural variability in the eye cannot be used in helping to "pigeon-hole" an animal in the evolutionary scale. Nature has produced certain special adaptations for diurnal or nocturnal vision whether they exist in fish, reptiles, birds, lemurs, or monkeys.

*Epithelial Pigment Layer*

The epithelial pigment layer (Figure 1, layer 2) which lies between the choroid and the visual cells has long since been of interest because of its supposed function. In the eyes of some forms (particularly fishes, amphibia, and birds) the pigment migrates down over the visual cells in light and contracts back into the body of the epithelial cell in darkness. In these same forms the cone myoid contracts in the light and



a b

FIG. 9. Photomicrograph of the pure rod retinas of nocturnal lemuroids (*a*) Galago mala and (*b*) *Nycticebus tardigradus*. × 630.

elongates in the dark; the rod myoid elongates in the light and contracts in the dark. Much has been written concerning the supposed functional significance or adaptiveness of these phototropic responses (see Arey, 1915). Herzog (1905) and also Exner and Januschke (1906) maintained that these changes represent a mechanism for adaptation of the eye to day, and to twilight, vision. In dim light or in darkness when the rods are to function, the pigment moves back toward the cell body and leaves free the spaces between the rods, resulting thereby in a less complete insulation of these elements. Under these conditions, greater stimulation is obtained than if they were covered by a thick mantle of pigment, in which case only the light which passes through the retina in the direction of the long axis of the rods could enter them. The majority of the cones under these conditions are not functional on account of their high thresholds, and they elongate and thus move out of the way. The rods contract so that optimum conditions are presented for their stimulation.

In bright light the pigment moves forward (toward the external limiting membrane) and protects the rods which have low thresholds. The rods elongate, whereas the less sensitive cones are drawn out of the pigment by their contractile myoids, and are thus made freely accessible to the stronger light. Examples of the light-adapted and

dark-adapted retinas of the frog showing the difference in the position of the pigment are illustrated in Figures 12 and 13.

Garten (1907) maintained that the function of the expanded pigment is to absorb all light which might escape from the visual cells by refraction; that were it not for the optical isolation of the visual cells by the pigment a great deal of light would be scattered in all directions on account of the large ellipsoids (such as occur in fishes) and the strongly refractive oil drops (amphibians, reptiles and birds). In the

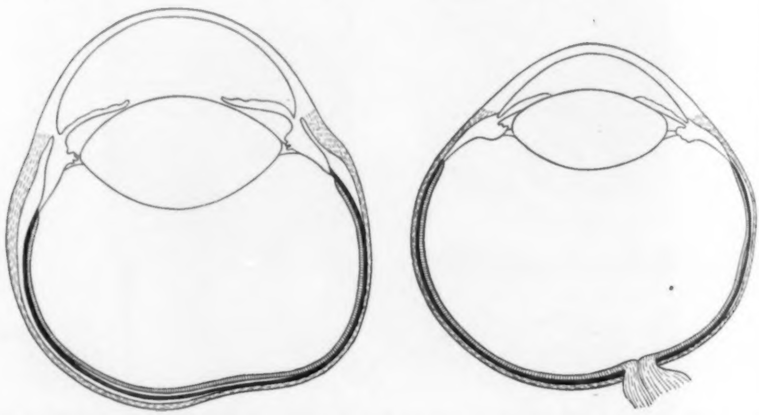


FIG. 10 (*left*). Meridional section of the eye of the nocturnal lemuroid, *Nycticebus tardigradus*. Note extremely large curved cornea, large lens and relatively small vitreous chamber.

FIG. 11 (*right*). Meridional section of the monkey eye of *Macaccus rhesus*. Compare with figure 10.

long, slender rods, such as occur in mammals, total internal reflection prevents this dispersion of light. This is an interesting observation and appears to be worthy of consideration. In pure rod retinae where the rods are long cylindrical structures, pigment is usually sparse or entirely lacking (e.g., dogfish, rat, bat, lemurs, nocturnal monkey). In the Gecko, which contains rods only but with the rods possessing a well-developed "barrel-shaped" ellipsoid and a large paraboloid, the pigment is very abundant and almost completely surrounds the outer segments (cf. Figures 6 and 9). The amount of pigment varies greatly but, in general, it is sparse in nocturnal animals. There has never been any decisive evidence that pigment migrates in the mammalian and human eye; yet we see statements in modern textbooks of human physiology that ascribe to the human eye these phototropic responses which so typically take place in the eyes of lower vertebrates. Even if the pigment did migrate in the human and anthropoid eye, it could hardly

serve to absorb scattered light, for it is relatively sparse as compared with lower forms. For this same reason it could hardly also serve to help adapt the retina for strictly nocturnal or diurnal vision. Although the matter of pigment migration has been studied under a great variety of experimental conditions, so far as I know, no one has really solved the problem adequately as to the significance of this process. From my own observations I am strongly inclined to the view of Garten. This

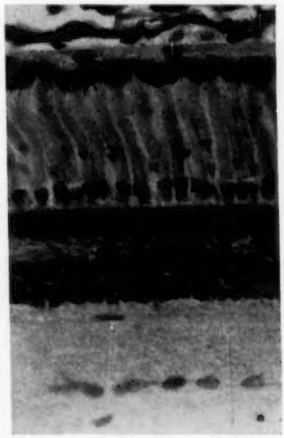


FIG. 12 (*left*). Photomicrograph of light-adapted frog retina, showing expanded (migrated) epithelial pigment. × 300.

FIG. 13 (*right*). Photomicrograph of dark-adapted frog retina showing contracted epithelial pigment. × 300.

is based upon a correlative study of the shape of the visual cells and the amount of pigment present.

Welsh and Osborn (1937) have shown that, in the catfish eye, dark-adaptation characteristically takes place during the night time, but not during the daytime even though the animal be kept in darkness. During the daytime the eyes kept in darkness tend to adopt the typical light conditions at sunrise and return to the dark position at sunset. Thus they have demonstrated a diurnal rhythm. If the existence of similar persisting diurnal rhythms are to be demonstrated in the eyes of other vertebrates, it is apparent that many measurements, which have been made in the past on positional changes of the pigment and the visual cells, may be subject to modification.

### *Retinal Structure and Visual Acuity*

Those who are acquainted with photography are aware that the fineness of detail that a photographic plate can register depends upon

the fineness of the emulsion. If the particles are fine and close together, one obtains much greater detail than when using a coarse emulsion with particles large and farther apart. This is a situation comparable to that found in the retina. A low visual acuity signifies that the average distance between the active retinal elements is large, whereas a high visual acuity means that the distance is small. In this respect the vertebrate retina varies greatly in its structure. Not only does it vary in eyes of different animals but, within the same eye, the elements vary in size and closeness. In the fundus of the eye the visual cells are always finer and more closely packed than toward the peripheral regions. Since, however, the number of rods and cones is fixed structurally in any given region of the eye, it is apparent that the number of elements per unit area must vary functionally in order to mediate the great variation in visual acuity accompanying changes in illumination. This has been shown physiologically by a number of investigators. With lowest illumination, vision is primarily a function of the rods. As more and more rods reach their thresholds and become functional, visual acuity increases. With still further increase in illumination more cones come into function, but vision is still mediated by the rods because there are more active rods than cones. Presently, however, with further illumination, visual acuity becomes determined entirely by the cones, and the gradual augmentation of the numbers of functional cones will continue until all are active and no further change in visual acuity is possible. The threshold distribution of rods and cones according to Hecht (1928) is given in Figure 14. The curves are based upon the data obtained by Koenig in his quantitative studies upon brightness discrimination.

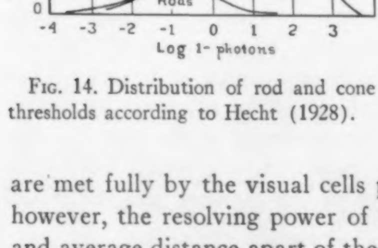



Fig. 14. Distribution of rod and cone thresholds according to Hecht (1928).

It is apparent, therefore, that the requirements for the large variations in visual acuity cannot be met by the structural make-up of the retina alone, and that they are met fully by the visual cells possessing different thresholds. Since, however, the resolving power of the retina depends also upon the size and average distance apart of the photosensitive elements, it is apparent that vision must vary greatly in different animals. In fishes and amphibians the visual cells, particularly the rods, are distinctly larger and further apart than in the mammals. Even within the mammals them-

selves, the size and average distance apart of the rods varies in different animals. Also in all animals with a double retina the cones are always more numerous per unit area in the fundus than toward the *ora serrata* where the rods become increasingly denser.

In the pure cone retina of the turtle and in other forms, there is a small area in the optical axis of the eye where the cones are distinctly smaller and more numerous than in the remainder of the retina. The increased numbers of cone nuclei, therefore, cause a bulging and thickening of the external nuclear layer (Figure 1, layer 5). This thickened region is called the *area centralis retinae.* The localized concentration of numerous smaller elements in this area presents a structural condition enhancing greater visual acuity than in those eyes where it is absent.

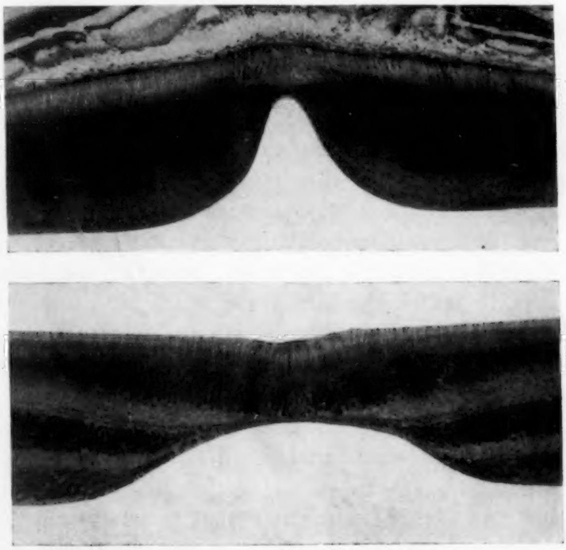


FIG. 15 (*above*). Photomicrograph of the fovea centralis of the chameleon. × 50.
FIG. 16 (*lower*). Photomicrograph of the fovea centralis of the marmoset. × 100.

In the eyes of practically all vertebrates, and particularly those of the mammals, the fundus shows some structural specialization for increased visual acuity, the acme of this specialization is reached in those animals possessing a fovea. The fovea consists of a more or less marked retinal depression in the visual axis of the eye. The nuclear layers are displaced laterally, and by reason of a marked increase in the number of visual cells, the external nuclear, and internal nuclear layers become thickened (Figures 15 and 16). The fovea is devoid of rods; and the

cones by reason of their greatly increased numbers per unit area typically become long, slender, and closely packed and thus look more like rods. The visual elements are more closely packed in some foveas than in others; this apparently signifies a greater visual acuity. When one compares the highly developed foveas of diurnal lizards and rapacious birds with those of the anthropoids and man, one can only conclude that, in the former, the conditions for high visual acuity are more nearly met than in man.

In the chameleon fovea, the elements are very closely packed and the foveal depression is so deep that all of the nuclear layers are displaced laterally (Figure 15). In the fovea of the marmoset (also in Rhesus monkey and in man) the depression is not nearly so deep, the external nuclear layer is continuous over the foveal pit and the cones are not as fine as in the chameleon retina (cf. Figures 15 and 16). Foveas occur sporadically throughout the vertebrate series. According to Kahmann (1936) they are present in certain salt water fishes. In these forms the fovea is lateral rather than central. They are typically present in diurnal lizards, in birds (particularly the rapacious birds) and in most anthropoids including man. Some birds possess, in addition to a central fovea, a lateral or temporal fovea (e.g., the swallow). It has been stated that the hawk possesses about one million cones per square mm. at the fovea. In the human eye there are supposed to be 140,000 to 160,000 cones per square mm. Based on the fineness of the foveal elements, therefore, the bird eye is much more efficient than the human and, I think, experience bears this out, for we are all acquainted with the marked visual acuity which the birds exhibit. Nevertheless it must also be recognized that the resolving power of the retina is limited by the diffraction pattern and this in turn depends upon such factors as size of the aperture and the distance from the lens to the receiving surface.

Dr. Elliott-Smith (1928) attributes the changes occurring in the structure of the parts of the anthropoid brain concerned with vision, as due to the origin of the macula, which is also, according to him, responsible for the profound evolution of the nature of vision in apes and man. He attributes the development of the true macula as intimately associated with the altered position of the eyes and the almost overlapping of the visual fields. In this connection he says, "Before this important change can take place in the retina all the fibers coming from the temporal side of the retina should remain uncrossed, for the macular area develops in the line where the temporal and nasal fields of the retina meet, and one-half of it transmits fibers which remain uncrossed, and the other half transmits fibers which cross to the other

side of the brain. Hence until the rearrangement of the fibers in the optic chiasm has been completed, the true macula cannot develop. Intimately linked with this process of evolution is the development of a wide range and a greater exactitude in the conjugate movements of the eyes." The assumption that the true fovea cannot develop until the optic fibers become arranged is not substantiated, for a very prominent fovea centralis develops in the lizards where there is complete crossing of the optic tracts, and a fovea lateralis is present in many salt water fishes where there is also complete crossing. In amphibia with complete decussation, there is no fovea, so it cannot be said that the development of the fovea is in any way intimately bound up with any particular arrangement of crossed and uncrossed opticus fibers. The belief that the development of a wide range and a greater exactitude in conjugate movements is intimately linked with the foveal development is not borne out, for the chameleon, although he may enjoy temporary binocular vision, exhibits marked independent movements of the eyes and probably, for the most part, uses only monocular vision. Whereas foveal development and the ability to move the eyes seem to go together, conjugate movements are not necessarily implied, nor is binocular vision. In this connection Kahmann (*op. cit.*) points out that the presence of a fovea in so many animals, among which a binocular use of the eyes is never made, shows us how much more monocular vision predominates. Foveas appear to represent mechanisms for increased visual acuity be they present in fishes, lizards, birds, monkeys or man, and their presence is apparently not specifically related to any definite arrangement of the opticus fibers nor restricted to conjugate movement of the eyes.

Walls (1937, 1940) has advanced stimulating ideas regarding the significance of the foveal depression. It has generally been regarded that the attenuation or displacement of the retinal layers at the fovea presents a condition whereby light may reach the foveal cones unimpeded, i.e., without passing through the ordinarily present layers of the retina. He justly calls attention to the fact that in an afoveate area centralis, the retina is thicker than the less specialized retina beyond its limits—yet, in spite of this, the resolving power of the area centralis retinae is obviously much greater, thus indicating that the production of a thin spot *per se* is apparently not so important. He produced evidence to indicate that the foveal clivus refracts the light, thus broadening the retinal image and bringing into play a larger number of visual cells than would otherwise be the case. By reason of this optical property there thus occurs at the fovea a mechanism that increases the resolving power over that produced by the afoveate area centralis.

This idea requires that the refractive index of the retina be higher than that of the vitreous—an assumption which Walls originally made but which he was able to support later from the measurements of Valentin (1879). It is apparent, however, that the shape of the foveal clivus (convexiclivate) in reptiles and birds (Figure 15) is more efficient in this respect than in the low (concaviclivate) foveas of the anthropoids and man (Figure 16). From the data which Walls employs he suggests that "the human fovea has degenerated like that of Sphenodon, the owls, and the pigeon, from a once much more deep and abrupt depression."

*Retinal Photopigments*

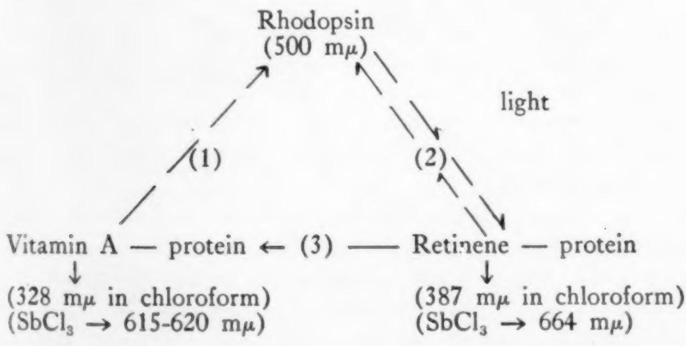
The association of visual purple, or rhodopsin, with the visual function of the rods has long been known. This photosensitive substance was discovered in 1876 by Franz Boll. It was later studied in much detail by Kühne (1877), who termed it visual purple or rhodopsin. Koenig first showed the relation between the visibility curve at low illumination and the absorption spectrum of visual purple. Many added physiological facts have completely supported the early formed inference that visual purple is concerned with rod vision. We know that when a dark-adapted retina is exposed to light, its color fades from a rose to an orange-yellowish color and finally to white. If it is placed back in the dark it will regenerate its original rose color. Some observers claimed that it will regenerate only in the dark if the retina is accompanied by the pigment epithelium, thereby favoring the idea that the pigment cell is responsible for its generation. Although Kühne (*op. cit.*) reported that visual purple in solution will regenerate some of its color, this observation apparently has never been confirmed until recently by Hecht (1936) and his co-workers. Boll (*op. cit.*) observed that the pigment epithelium in frogs firmly adheres to the retina when exposed to light, thus implying some functional relationship between this tissue and visual purple. The carotenoid nature of this photopigment, first suggested by Boll, has recently been confirmed by Wald (1935, 1936). He showed that, in the frog, the pigment epithelium contains large stores of vitamin A and xanthophyll esters. Since the presence of vitamin A is known to be definitely essential to the production of visual purple, it becomes apparent that the storage of this substance in the pigment epithelium firmly establishes an important relation between this layer and the retina proper.

The condition of night blindness has been known for ages, and its relation to poor nutrition recognized. It was seen in men returning from long sea voyages, in people living in prisons, and among Orthodox Russians during Lenten fasts. The use of liver as a cure has been wide-

spread. According to Tansley (1931) the earliest reference appears in Eber's Papyrus dated about 1500 B.C. Liver treatment was apparently recommended by Hippocrates.

Fredericia and Holm (1925) and Tansley (1931) showed that animals deprived of vitamin A become abnormally insensitive to dim light (night blind), due to the failure to synthesize visual purple. In recent years the problem of vision in relation to vitamin A has been studied both in animals and man by a number of investigators, particularly by Wald (1939), who has shown that vitamin A is the precursor of visual purple as well as the product of its decomposition.

Dark-adapted retinas are rose-colored due to their rhodopsin content. In light they bleach to an orange color. This orange-colored substance in neutral fat solvents yields a yellow lipoid pigment which Wald called retinene and which is a carotenoid. In aqueous solution, retinene with a protein are the final products of bleaching. In the isolated retina the orange color fades and the tissue becomes colorless. The extracts of completely faded retinas are also colorless. They contain no retinene, but a large quantity of newly formed vitamin A: the final product of bleaching. The same is achieved by prolonged illumination of the intact retina. In the living animal placed back in darkness, vitamin A is re-synthesized to rhodopsin. The retinal cycle is thus represented by Wald in the following form:




Although the above is the cycle for most vertebrates, Wald has shown that in fresh water fishes the photopigment has a purplish color which, in aqueous solution, has an absorption spectrum with its maximum at 522 mμ instead of 500 mμ for rhodopsin. This substance, which Wald has termed porphyropsin, breaks down in light to a russet colored product called by him retinene$_2$, and which in the retina is transformed further to a new pale yellow carotenoid that yields with antimony chloride a band at 696 mμ and which has been called vita-

min $A_2$ in contrast with vitamin A in the rhodopsin system which gives a band at 615-620 m$\mu$ in antimony chloride. This porphyropsin system is illustrated below.

$$
\begin{array}{ccc}
 & \text{Porphyropsin} & \\
 & (522\ \text{m}\mu) & \\
\nearrow & & \searrow\!\!\nwarrow \quad \text{light} \\
\text{Vitamin } A_2 \text{ — protein} & \leftarrow & \text{Retinene}_2 \text{ — protein} \\
\downarrow & & \downarrow \\
(355\ \text{m}\mu \text{ in chloroform}) & & (405\ \text{m}\mu \text{ in chloroform}) \\
(\text{SbCl}_3 \rightarrow 696\ \text{m}\mu) & & (\text{SbCl}_3 \rightarrow 706\ \text{m}\mu)
\end{array}
$$

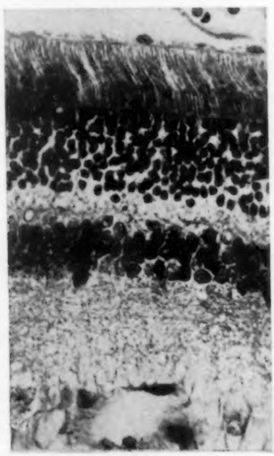
The difference between the two systems apparently lies in the fact that in the porphyropsin system there has been added one ethylenic link (— CH = Ch —) in the polyene chain-yielding formula $C_{22}H_{32}0$ as against $C_{20}H_{30}O$. This is sufficient according to spectrophotometric studies to shift the spectrum 20-30 m$\mu$ toward the red (Wald, 1939).

Whereas all fresh water fishes examined were found to possess porphyropsin systems only, Wald discovered that those fishes which spawn in fresh water and live normally in the sea (anadromous) possess, primarily, the porphyropsin system, whereas those which live mostly in fresh water, but spawn in the sea, possess primarily the rhodopsin system. These euryhaline fishes, as a group, thus possess either predominately or exclusively that photopigment and that vitamin A ordinarily associated with the environment in which the fish is spawned. It appears then that one particular pattern of vitamin A which an animal possesses is not primarily an environmental response, but is fixed genetically.

Very little is known about the photopigments of the cones, but it is of interest in this connection to state that Wald (1937) has studied spectroscopically, and partially isolated from the chicken retina, a cone photopigment, which he has called iodopsin and which has an absorption spectrum-maximal at about 575 m$\mu$.

Not only has vitamin A deficiency been found to raise the visual thresholds (particularly for rod vision), but recent experiments have been made to show that rats suffering from avitaminosis A undergo structural breakdown of the retina. The extent of the degeneration is variable and depends apparently upon the degree of the deficiency (Tansley, 1933, 1936; Johnson, 1939). Miss Johnson has shown that degeneration may be mild, involving only the outer segments of the rods (v. Figure 1) or it may be so progressive and severe as to involve

the visual cells, the external limiting membrane, the outer nuclear layer, the outer molecular layer, and the internal nuclear layer. Such severity also involves the pigment epithelial layer (cf., Figures 17 and 18). In such severe cases of degeneration, apparently the ganglion cell layer is not involved. She obtained some evidence to show that, when only the outer segments of the rods were involved (and not the nuclei), there were indications of regenerative processes when the animal was put on a recovery diet. Further evidence definitely to establish this point is necessary. The degenerative changes observed in mammalian eyes, therefore, as a result of avitaminosis A, are of extreme importance.



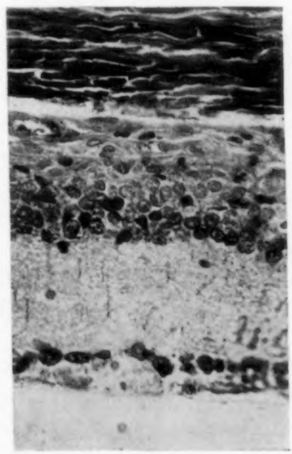


FIG. 17 (*left*). Photomicrograph of the normal rat retina. × 325.

FIG. 18 (*right*). Photomicrograph of the rat retina, showing marked degeneration resulting from extreme vitamin A deficiency. The visual cells and their nuclei (external nuclear layer have disappeared completely. (From M. L. Johnson, 1939.) × 325.

They raise the question whether in certain cases of human night blindness, resulting from vitamin A deficiency, there may not be some similar degenerative changes of the rods. Might this not be the case in certain individuals who either respond very slowly or fail to respond at all to large doses of carotene? The ability to respond, of course, would depend upon the extent of damage when treatment is administered. This is hypothesis but is certainly worthy of consideration.

In summary it may be said that, as the eyes of various animals are viewed from a morphological point of view, one is impressed by the fact that, though they are all constructed upon a common generalized plan, nature has deviated considerably from this common architectural

(*Continued on page 142*)

# MAN'S PHYSICAL ENVIRONMENT AND MAN'S BEHAVIOR[1]

By Kirtley F. Mather
Harvard University

THE geologist views man as an inhabitant of the earth. Like its other inhabitants, man is a product of evolutionary processes operating on this particular planet. Such ancient philosophic concepts as those implied by the classical myth of Hercules and Anteus, and the reference in the Hebrew scriptures to the fact that man was made of "the dust of the ground," are just as valid today as ever before. In a very significant sense, we are the sons of the earth. The geologist's reference to "Old Mother Earth" may be figurative, but it reveals an attitude of mind that leads to extremely salutary results. That approach to the study of man may strip some of the glamor from the object of our study, but it is realistic, revealing, and in the last analysis, reassuring.

We may be the latest product of the creative forces displaying themselves in the organic development of this particular portion of the cosmos, but we have no reason to assume that we are the last achievement of those forces. Nor does the fact that man has arisen from a lowly origin through processes of evolution validate the optimistic inference that he will necessarily continue his progress to ever higher levels of activity. Evolution does not guarantee progress; it merely guarantees change. The change may be for the better or the worse, depending upon the conditions of time and place and the vitality of the individuals concerned.

The pages of Mother Earth's diary reveal an amazing and thought-provoking record of the progress of living creatures throughout the long eras of earth history. Again and again, in the procession of the living, dynasties of animals or plants have arisen from a humble origin to a position of world supremacy, maintained for a comparatively brief period and then lost forever. Some have disappeared entirely as their paths have led them off into blind alleys. Others have sunk to a low level and have continued a degenerate existence to the present day. A few have given rise to other and more efficient forms of life which superseded their predecessors as leaders in the procession. We are gradually

[1] Presented before the Union College Symposium "Science Views Man," March, 1941, and based, in part, upon the 1939 Sigma Xi Lecture, published in vol. 28 of the Quarterly.

discovering some of the reasons for success and failure along the path of life. Beyond question, man may profit from those experiences of the past, if he uses the intellectual and moral resources that are available to him.

The first record of living creatures dates back a billion years and indicates that one-celled organisms first appeared in what the geologist calls Pre-Cambrian time. Consisting of but a tiny drop of jelly-like protoplasm enclosed within a cell wall, these lowly creatures displayed in simplest manner the essential characteristics that distinguish living from non-living matter. They utilized energy, derived either directly from the sun or indirectly from the food that they ingested, to defend themselves against the destructive forces in their environment, to grow in size, and to reproduce their kind. They were aware only of objects that came in direct contact with their bodies, and possibly also of changes in the intensity of light such as that between sunlight and darkness. They acted automatically when stimulated by physical impact. They reproduced by fission; the one cell grew to somewhat larger dimensions than usual and then split into two complete individuals, neither of which could be called parent or offspring, for both were equally mature as they separated, each to go its own way, utterly regardless of the other. There was no thought nor emotion, no capacity for exalted feeling; the principle of life was operating at the lowest possible level.

But there was much progress during the next few hundred million years. By the opening of the Cambrian period, roughly half a billion years ago, a widely diversified assemblage of highly organized animals had come into existence. Many of them possessed a well-coordinated nervous system, specialized organs for locomotion and reproduction, as well as eyes and antennae, structures that gave them the ability to be aware of objects at some little distance from their bodies. With the advent of sexual reproduction, there was established the basis for emotions involving others than oneself and the foundations upon which social relationships could later be developed. The development of the nervous system similarly was the first step toward the emergence of thought as a determining factor in the process of evolution.

Take the Cambrian trilobites as suggestive of the highest achievement of creative evolution in that far-distant geologic period. Their individual actions were almost certainly not entirely automatic responses to external stimuli. On occasion, their behavior undoubtedly was in the category of reactions known to modern psychologists as the conditioned reflex. That means that whether or not they could think, they at least could learn from experience. Instinct is a far cry from reason, but the

record unquestionably indicates that instinctive behavior was perfected long before rational conduct was even attempted and may well have been its necessary precursor.

Certain associations of trilobite fossils in the Cambrian rocks suggest, but by no means prove, that group life was established as the natural order of existence for this kind of creature at that time. But group life does not necessarily mean social organization. Colonies of coral polyps were building reefs in the Paleozoic seas soon after the close of Cambrian time, but then as now those polyps were completely individualistic in their behavior. Although living in closely crowded groups, there was not the slightest suggestion of mutual aid or reciprocal forebearance. Each rugged individualist among the coral colonies sought only to preserve its own existence, competing with its fellows for food and oxygen, building its protective exoskeleton upon the dead bodies of its comrades, utterly regardless of the welfare of the other members of the colony. There could not have been and presumably there never will be a sociology of coral polyps. On the other hand, there well may have been a sociology of the trilobites, faintly foreshadowing the more perfect social organizations of their fairly close relatives, the insects.

Certainly by the end of the Paleozoic Era, approximately two hundred million years ago, social life had begun to emerge from the antecedent group life among the primitive insects of that time. But insect society developed along lines that diverged more and more from the trend that may be traced among the vertebrates, leading at last to those relationships that have profoundly influenced the spiritual phase of human life. As far as social organization is concerned, the insect societies reached a plateau of achievement several million years ago. There are no greater heights for them to ascend. Complete regimentation and thoroughgoing standardization of form and behavior have stifled individual initiative and barred all avenues of further progress.

On the other hand, progress toward truly social life as distinguished from mere group life was slower among the animals with a backbone than among the invertebrates. The first fossil fishes date back about four hundred million years and are followed in the geologist's timetable by amphibians and reptiles in turn. By the end of the Paleozoic Era these three subdivisions of the vertebrates were abundantly represented among the inhabitants of sea and land. Many species of each were undoubtedly accustomed to group life as exemplified by the "school of fish" or the "nest of reptiles," but there is no evidence of anything worthy to be called a society. Rare indeed is the suggestion of mutual aid, even as between parent and offspring. The coral-polyp principle of life, feeling, and action seems to have been the order of the day.

Among vertebrates that principle reached one of its most spectacular climaxes in the rapacious, carnivorous dinosaurs that ruled the lands during much of the Mesozoic Era, an interval of time that extended from about two hundred million to about seventy-five million years ago.

But even during that era while cold-blooded, small-brained reptiles were lords of the land, masters of the sea, and rulers of the air, the mammals made their appearance in the record of life development. They were small creatures, seemingly weak in comparison with the contemporary reptiles, but they cared for their offspring during days or weeks of helpless infancy and their brains were well nourished and efficient. The capacity for mother-love is not confined to this class of animals, provided as they are with glands for suckling their young; it appears also among birds and is displayed by some of the reptiles. But among the mammals it is well-nigh universal and has reached its most complete development. It may, therefore, be truly said that mother-love, in the real sense of the term, first appeared on earth about a hundred and fifty million years ago, the date of the oldest mammalian fossils.

Its advent marked a notable advance toward the principle of life, feeling, and action in man, the spiritual rather than merely the physical products of the evolutionary processes. It is no accident that nearly all mammals are gregarious; cattle run in herds, coyotes hunt in packs, beavers dwell in communal houses, mice live as families, men organize themselves in clans, tribes, and nations. Not until the physical structures characteristic of the mammals had emerged from their precursors among the reptiles could there be any "capacity for exalted or noble emotions or feelings."

The mammals, moreover, possess in their four-chambered hearts the only efficient mechanism for providing abundant nourishment to the brain, regardless of day or night, heat or cold. In them is found for the first time an opportunity for the development of the capacity to think, to learn by processes that transcend the acquisition of conditioned reflexes, to imagine in advance the consequences of contemplated action. Cooperative behavior, undergirding social organization of group life, finds in the mammals a wholly different basis than that which is fundamental in the insect society.

For nearly a hundred million years the mammals made little progress, either in numbers, diversity or attainments. A trivial minority of the land population, individually weak and puny, they were well-nigh submerged beneath the heavy weight of the powerful majority, the numerous and varied reptiles of the Mesozoic Era. Perhaps that long and bitter experience was necessary for the perfecting of the art of coopera-

tion, the embedding of the habit of mutual aid until it became an ineradicable element of mammalian nature. At any rate, it was not until the extinction of the dinosaurs and many of their kin, as the Mesozoic Era closed and the Cenozoic Era opened, that mammals entered their golden age.

During the first period of the Cenozoic Era, about seventy-five million years ago, mammals became the dominant form of life on the land. They possessed inherently valuable abilities that gave them superiority over the reptiles whose long supremacy came to an abrupt end. Tried in the balances of creative evolution, they triumphed where their competitors failed. Success for them could not possibly have been based upon mere physical superiority. In comparison with the dinosaurs, superbly armed for offense or defense in physical combat, they were almost pitiably weak. Only in those intangible qualities of mother-love and adeptness in the art of cooperation could their virtue have resided. "High mindedness, noble warmth of feeling, spirit or courage" was beginning to come into its own.

Even so, some of the mammals had their fling at the attempt to gain security by means of huge bulk and powerful armament. Several different strains at various times during the Age of Mammals evolved along lines that were essentially parallel to those previously pursued by the dinosaurs. Although each was locally and temporarily successful, all have long since become extinct or, like the rhinoceros, have been greatly reduced in their geographic spread, even before man appeared upon the scene. There is evidently something in the total environment that weighs the balances heavily against the dinosaur way of life.

It is of course noteworthy that mutual aid and cooperation were increasingly stressed by the successive members of the mammalian line that led at last to man. For millions of years our direct ancestors were in frequent and immediate competition for survival with sabre-toothed tigers and many other equally rapacious beasts of the field, forest, and jungle. Victory was won not because of stronger muscles, sharper claws, more powerful talons or greater bulk, but by virtue of skillful use of sticks and stones and fires; of clever planning for offense and defense; of superior organization of individuals into a social group; of thorough-going acceptance by each individual of his share of responsibility for the welfare of his fellows. The habit of cooperation, the capacity for sharing, the ability to think, and the attribute of ingenuity were thus firmly established in the very fibre of our ancestral lineage and have inevitably affected the "principle of life, feeling, thought, and action in man." Ours is indeed a goodly heritage. We do well to applaud the exploits of those remote ancestral anthropoids, who blazed

the trail of progress in ways that won the approval of the creative power eternally operating throughout the universe.

Such an interpretation of the record of geologic life development indicates that the spiritual part of man, like the physical part, is a product of evolutionary processes long operative on the surface of the earth. The human spirit is not an immigrant from some other sphere; it is indigenous to the environment in which we find it. Here it was cradled and nurtured, here it may grow to fulness of stature. Of all the ways of life that have thus far been tried by the creatures of the earth, that characteristic of mankind has been most highly approved in principle by the total resolution of all the forces, both measurable and intangible, that are effective in the processes of creative evolution.

From the point of view attained through knowledge of geologic life development, man has today a unique opportunity to gain continuing security for himself and his progeny on the face of the earth, but whether or not he takes advantage of that opportunity is to be determined largely by himself. So far as we can tell, man is the first animal possessing the power to determine his own evolutionary destiny, but there is nothing in the record that guarantees that he will use that power wisely.

The animal species that in the past have been able to maintain their existence for more than two or three million years are relatively few in number. Most of them were comparatively simple types belonging to the less highly organized branches or phyla of the animal kingdom. Many were inhabitants of the sea where environmental conditions were remarkably stable throughout long periods of time. Among placental mammals, the major subdivision of the vertebrates to which man belongs, there is no similar record of longevity. Except under extraordinary conditions of geographic isolation, no species of placental mammal has persisted more than two or three million years. No matter how successful it may have been temporarily in multiplying and spreading over the face of the earth, each has become extinct in a geologically brief span of time. Perhaps a half million years might appropriately be taken as the average "life" of a species in this group of highly organized and notably complex creatures.

But extinction does not necessarily mean failure; it has frequently indicated the acme of achievement. For example, some of the now extinct three-toed horses and four-toed camels passed on "the torch of progress" to their descendants, the one-toed horses and two-toed camels, and thus gained long-continuing security for their kind.

What, then, does the future hold for mankind? The genus *Homo* has already existed for three or four hundred thousand years; the

species *Homo sapiens* has about fifty thousand years to its credit. If the average applies, we may expect nearly or quite a half million years more of existence for our kind and then either oblivion at the end of a blind alley or progressive development into some type of descendant better adjusted than we to the total environmental factors of the time.

But does the average apply? Must man exit from the scene through either of the doors—that which closed behind the dinosaurs and titanotheres or that which opened before the three-toed horses and notharctines?

Most animals tried to gain security for themselves by specializing in adjustment of structure and habit to particular environmental conditions, whereas man is a specialist in the adjustability of structures and habits to a variety of environments. No other vertebrate can live as can he, on Antarctic ice cap, in Amazonian jungle, beneath the surface of the sea, or high in the air.

Furthermore, man is the world's foremost specialist in transforming environments to bring them within the range of his powers. Far more efficient than the beaver or the mound-building ant, he drains the swamp, irrigates the desert, tunnels the mountain, bridges the river, digs the canal, conditions the air in home, factory, and office.

As a matter of fact, adjustability to environment is accomplished more by controlling surroundings than by modifying internal organs or essential functions of the body. When we ascend with Major Stevens into the stratosphere, or dive with Doctor Beebe 500 fathoms deep off Bermuda, or live with Admiral Byrd through the long night of Little America, we take along with us a sample of sea-level atmosphere and temperate climate that is our real environment in a situation otherwise unbearable. Fur-lined parkas and tropical linen suits are but media for ensuring an immediate environment as nearly as possible like that of middle latitudes when living in polar or equatorial surroundings.

But regardless of interpretation of procedure, the result is clear. Man has placed himself in control of external conditions to an extent immeasurably greater than any other creature. He has practically "drawn the teeth" of environment.

Although we know little of the details, it is certain that most of the creatures of the past who "have had their day and ceased to be" were forced into extinction by changes of one sort or another in their environment, changes that came with such relative speed that they were unable to make adjustment to them in time. Man need have no fear on that score.

It is, however, immediately apparent that man's conquest of his surroundings has resulted from his clever use of things. Unless there is a ceaseless flow of cotton, flax and wool, of coal, iron and petroleum, of copper, lead and tin, from ground to processing plant to consumer, he becomes a puny weakling. It is because he uses certain resources provided by his environment that he is freed from slavery to his environment. Are these resources adequate to keep him supplied with what he needs to maintain indefinitely the sort of existence to which he has accustomed himself?

There are two fundamental sources of the goods and the energy that man uses in the grim business of securing the sort of living that he apparently desires. On the one hand, there is the farm and the waterfall, on the other there is the mine and the quarry. Things which grow in the field or forest, and power produced by falling water are in the category of annual income. Now that scientific research has made available the limitless quantity of nitrogen in the air for use as fertilizer, the resources of the plant and animal kingdoms are renewable; we use them, but we need never use them up. In startling contrast, the resources of the mineral kingdom are non-renewable; they are in the category of accumulated capital. Petroleum and coal, copper and iron, lead and vanadium, these and many other prerequisites of modern civilization have been accumulated by nature through hundreds of millions of years of geologic activity. Thanks to scientific research, man is exhausting that store of mineral wealth in a few hundred, or at most a few thousand years. That inescapable fact is at rock bottom one of the most fundamental causes of economic distress, of war between nations and of strife between classes.

Fairly accurate estimates of the world stores of many non-renewable resources are now available. For nearly all the important non-renewable resources, the known world stores are thousands of times as great as the annual world consumption. And for the few, which like petroleum are not known to be available in such vast quantities, substitutes are already known, or potential sources of alternative supply are already at hand, in quantities adequate to meet our current needs for at least two or three thousand years. There is, therefore, no prospect of the imminent exhaustion of any of the essential raw materials, so far as the world as a whole is concerned, provided our demands for them are not multiplied rapidly in the future.

That, of course, raises another question. Will the demand for non-renewable resources increase materially in the future and thus hasten their exhaustion? Recalling the fact that the human population of the earth has increased almost five-fold in number in the last three hundred

years, we might well be fearful on that score. The study of current population trends, however, makes it readily apparent that the next few hundred years will by no means duplicate that record of the past. If present trends continue, the all-time maximum population of the United States will be attained about the year 1960 and will total little more than 150 million souls. Thereafter, except for possible influx of immigrants from other countries, no further increase in numbers is to be expected.

Accurate figures are available for only a few other countries, such as England, France, and Germany, but there is a strong probability that the all-time maximum for the "white" races will be reached during the last third of the twentieth century and for the entire population of the earth before the end of the twenty-first century. Although the human family has doubled its numbers since 1860, it is extremely unlikely that it will ever reach twice its present number of approximately two billion. The pressure of demand for non-renewable resources will not, therefore, become acute because of the increase in population in the near future. Mother Earth is a very wealthy benefactress; our heritage of physical resources is far greater than ordinarily supposed.

There is, however, another reason why current consumption of non-renewable resources cannot be taken as the basis for computing the "life" of such stores of basic materials. The demand for automobiles, telephones, radios, airplanes, zippers, is today very unevenly distributed. Only a small fraction of the human population uses such things in any large amount. Other peoples are beginning to demand them and will do so increasingly as they become acquainted with the "benefits of civilization." In a few decades, unless there is a return to savagery, the world demand for many non-renewable resources will be twice or thrice that of today.

Taking all these things into consideration, it would appear that world stores of needed natural resources are adequate to supply a basis for the comfortable existence of every human being who is likely to dwell anywhere on the face of the earth for something like a thousand years to come.

Even so, there may be found here an excuse for the policy of "grabbing while the grabbing is good," a policy that motivates many individuals and nations at the present time. That excuse might, of course, be offset by the suggestion that there is no need to take thought for a morrow a thousand years hence, if we have any respect for the ingenuity of our remote offspring. There is, however, another phase of current trends in human history that should not be overlooked in this connection.

One hundred years ago, something like 80 per cent of all the things man used had their source on farms; most of the energy used to do the work of the world came from the muscles of living beings and from falling water. Today only about 30 per cent of the things man uses come from things that grow; most of the energy with which work is done comes from petroleum and coal. For a century or more, the policy has been to use relatively less of the annual income and more and more of the stored capital.

Now comes the change. Automobile steering wheels are made from soy beans, piano keys from cottage cheese; innumerable articles fashioned of plastics are produced in part from corncobs and alfalfa; multitudinous metal and rubber substitutes are synthesized from various farm crops. Energy is transmitted at high voltages for hundreds of miles from hydro-electric turbines. A considerable portion of the annual budget for research is being devoted to progress in the direction of using more of the renewable resources—man's annual income—and less of the non-renewable resources—nature's stored capital.

What this new policy will mean is readily apparent. With progress along such lines, the pressure for political control of metalliferous ore deposits, coal fields, and oil pools is lessened. Much of the physical basis for international jealousy is liquidated. At last the intelligence of science may make it truly practical to "beat our swords into ploughshares, our spears into pruning hooks."

Again comes the insistent question from the pessimistic critic. Is there land enough? Is there sufficient fertile soil to provide adequate food and in addition the plant materials for the ever-expanding chemical industries? And again we hear the same reply. Yes, there is enough and to spare. J. D. Bernal computes from apparently valid data that the cultivation of two billion acres of land by the methods now in vogue in Great Britain would provide an optimum food supply for the entire population of the earth. Two billion acres is less than half the present cultivated area of four billion, two hundred million acres, itself hardly twelve per cent of the land surface of the earth. And in this calculation no account is taken of the increased yields that may confidently be expected from the continuing research of agronomists, plant breeders and experts in animal husbandry, not to mention recent developments in the new science of the soilless growth of plants. Evidently, the predictions of Malthus notwithstanding, mankind need have no fear that increasing populations will place an impossible burden upon the available sources of food. Human ingenuity, intelligent use of renewable resources, wise adjustment of structures and habits to environmental conditions, seem competent to dispel that dread shadow.

But these optimistic conclusions are based upon world statistics. They do not apply with equal force to the economy of any individual nation. No modern state embraces within its political frontiers a sufficient variety of geologic structures to give it adequate supplies of all the various metalliferous ores necessary for modern industrial operations. Likewise, none enjoys a sufficient variety of climatic conditions to permit all kinds of foodstuffs to be grown on its farms and fields or gathered from its forests, and to allow the growth of all the various plants contributing materials to industry. For the present and probably for a long time to come, every nation is dependent upon many other nations for resources that it needs for its own prosperity.

Perhaps the most important fact concerning the life of man today is this fact of interdependence. No nation, community, or individual can gain any lasting measure of security without taking that fact into consideration. The resources that man must utilize, if he wishes to escape the fate of his less intelligent relatives now known only by their fossil remains, are unevenly distributed and locally concentrated. The techniques of discovering and utilizing them are now fairly well known, but satisfactory procedures for making them and their products available to all members of the human family have not yet been established.

The critical question for the twentieth century is: How can two or three billion human beings be satisfactorily organized for the wise use and equitable distribution of resources that are abundant enough for all but are unevenly scattered over the face of the earth? Clearly, the future of man depends upon finding and applying the correct answer to that specific but far-reaching question.

And obviously the answer to that question can be found only if science and religion join forces in the search. The solution of our physical problems by scientific research brings us all the more forcefully into bruising contact with psychical and spiritual problems that must also be solved if man is to continue his existence on this planet. Fundamentally, organization of human society depends far more upon the nature of the human spirit than upon the physical characteristics of man. At the moment, the evolution of the soul is in much greater need of intelligent and devoted consideration than the evolution of the body.

Happily, the trend toward organization is recognizable throughout the entire range of cosmic administration. When men set themselves to the task of organizing their activities with the hope of improving the welfare of all mankind, they find that they are "in tune with the Infinite." Electrons, neutrons and protons are organized into atoms, atoms into molecules, molecules into compounds. Some of the compounds prove to be cells and some of these are organized to form indi-

vidual plants and animals. Latest of all in the history of creative evolution, certain individuals have been organized into societies. Transcending all that has gone before is the development of human society, obviously the most difficult, but potentially the most glorious organization yet attempted.

Organization means coordinated activity, and man has already demonstrated that he is a specialist in the art of coordination, despite the fact that every attempt at world organization thus far made has been bungled. There are two possible methods by which coordination of activities may be attained. One depends upon force from without, the other upon choice from within. The social group, whether it be the family, the industrial or commercial company, or the political unit, may be organized on the principle of regimentation, or it may be developed according to democratic principles. Both methods are being tried under a variety of conditions; the issue between the two has never before been drawn as clearly as it is today. Each has something to be said in its favor, but one stultifies the human spirit, stunts the soul; the other invigorates the human spirit, liberates the soul.

If regimentation be the choice of method for coordination of human activity, then the great mass of humankind must be trained for obedience—blind, unquestioning, but superbly skilful obedience. The educator becomes the intellectual and spiritual counterpart of the drill-sergeant in the army. This is no menial task, nor is its objective a mean one. Skill is a commodity of which there is never likely to be an over-supply. On the other hand, if democracy be the choice, the great mass of humankind must be trained for wise, self-determined cooperation. Precisely those qualities of mind and heart that have long been extolled in Christian doctrine must be developed to the fullest possible extent. Not only skill but also the ability to govern oneself, the eternal prerequisite for freedom, must be developed in each member of the group.

So far as the evolution of the human spirit is concerned, there is really no question as to which basis for the organization of human society is to be preferred. Regimentation may provide efficiently the goods required to meet the needs of the body for food and shelter and an opportunity to reproduce one's kind. But regimentation inevitably cramps initiative and confines ingenuity. It minimizes the worth of human personality and destroys the dignity of the individual. The question may sometimes be difficult to answer—whether it is better to starve as a free man or grow fat as a slave—but in the long run that question need never arise. Mother Earth is rich enough to nourish every man in freedom; it is man, not nature that enslaves. Worst of all, because it includes all, regimentation results in the stagnation of the stream of evolution. Even from the purely scientific point of view

this is enough to cause rejection of this method of developing coordinated activity. The record of the past is clear; stagnation among the mammals in every known instance has been soon followed by extinction. Regimentation may be satisfactory as a basis for long-continued existence among the insects, but it has never worked that way among the higher vertebrates. The conclusion seems inescapable that unless the human spirit continues to evolve in the direction indicated by past trends, toward ideals established in the very framework of the universe, even the human body will ere long be banished from the face of the earth. If man elects to live by bread alone, mankind commits collective suicide.

REFERENCES

BERNAL, J. D. The Social Function of Science. *Macmillan,* 1939.
BRADLEY, JOHN H., JR. Patterns of Survival. *Macmillan,* 1938.
FURNAS, C. C. The Storehouse of Civilization. *Columbia University Press,* 1939.
MANNHEIM, KARL. Man and Society in An Age of Reconstruction. *Harcourt Brace,* 1940.
MARETT, R. R. Head, Heart and Hands in Human Evolution. *Henry Holt,* 1935.
MATHER, KIRTLEY F. The Future of Man, etc. SIGMA XI QUART., vol. 28, no. 1, 1940.
PEARL, RAYMOND. Natural History of Population. *Oxford University Press,* 1939.
THORNTON, JESSE, *Editor.* Science and Social Change. Brookings Institution, 1939.
WARDEN, CARL J. The Evolution of Human Behavior. *Macmillan,* 1932.

## Some Biological Aspects of Vision

(*Concluded from page 129*)

scheme in many instances. Not only is this true of the photoreceptor mechanism, but with the light collecting and focusing devices as well. Thus nature's experiments stand before us to study and evaluate in terms of our knowledge and the applicability of physico-chemical laws.

REFERENCES

AREY, L. B. The Occurrence and the Significance of Photomechanical Changes in the Vertebrate Retina. An Historical Survey. *J. Comp. Neur.,* v. 25, p. 535, 1915.
ELLIOTT-SMITH, G. The new vision. *Trans. Ophth. Soc. United Kingdom,* v. 48, 1928.
FREDERICIA, L. S. and E. HOLM. Experimental Contribution to the Study of the Relation Between Night Blindness and Malnutrition. *Am. J. Physiol.,* v. 73, p. 63, 1925.
GARTEN, S. Die Veränderungen den Netzhaut durch licht. Graefe-Saemisch Handb. d. ges Augenheilk., I Teil, III Bd. XII Kap. Anhang, S. I, 1907.
HECHT, S. Rods, Cones and the Chemical Basis of Vision. *Phys. Rev.,* 17, 239, 1937.
JOHNSON, M. L. The Effect of Vitamin A Deficiency Upon the Retina of the Rat. *J. Exp. Zool.,* v. 81, p. 67, 1939.
KAHMANN, H. Uber das foveale Sehen der Wirbeltiere 1. Uber die Fovea centralis und die Fovea lateralis bei einigen Wirbeltieren. v. Graefe's Arch. f. Ophth., Bd. 135, S. 265, 1936.
TANSLEY, K. The Effect of Vitamin A Deficiency, etc. *Biochem. Jour.,* v. 30, p. 839, 1936.
WALD, G. Vitamins A and Vision. *The Collecting Net,* v. 14, No. 7, p. 1, 1936.
WALLS, G. Significance of the Foveal Depression. *Arch. Ophthal.,* v. 18, p. 912, 1937.

# DAYTON C. MILLER[1]

FOUR lectures are indelibly fixed in the writer's mind. One, heard when a boy, was by Walter P. Bradley and the subject was liquid air. An overflow audience crowded into the Hyperion Theatre, and Professor Bradley, with a milk can of liquid air, brought to town against the better judgment of the railroad, made "steam" in a tea kettle on a block of ice and shattered a sirloin steak as brittle as glass.

The second was Arthur H. Compton's address, "What Is Light?" Never were demonstration experiments and the projection lantern synchronized more effectively. Behind a long table the Nobel prize winner spoke with great assurance. Assistants brought off every demonstration successfully without apparent orders. The room was darkened and the pictures appeared on the screen at just the right moment—not one was upside down.

Another laureate in physics, Irving Langmuir, gave the third. He entered the crowded auditorium with a box of slides, but by oversight there was no lantern or operator. The audience never missed them. So graphic was the great man's description of his work with nonmolecular films, so simple was his language, that one wonders what possible addition the slides would have been. For supreme composure in a situation that must have changed the pattern of an important lecture, the incident was a memorable one.

Dayton C. Miller, physicist and flautist, was responsible for the fourth treat. He talked about sound on a stage crowded with every conceivable variety of flute-like instrument and much scientific apparatus. From the oat straw pipes of Arcadian shepherds and the reeds of the goat-hoofed Pan to the gold, silver, and glass flutes of a more sophisticated age he showed "the only way, since gods began to make sweet music, they could succeed."

For those who wished science with their music he spoke of pure tones, of harmonics, and overtones, of beats, dissonance, and unmusical noise. With a beam of light that danced merrily over a screen he showed the characteristic traces of all these sounds, and on the blackboard wrote equations in Fourier's series that froze music into mathematics. Surely, he insisted, there must be some elemental harmony between the beauty of line and the beauty of sound. On the screen he showed the most beautiful curve he knew, his wife's profile. Turned through ninety degrees it looked like one of the curves he had reproduced with the

(*Continued on page 148*)

[1] An editorial by George A. Stetson in *Mechanical Engineering*, 1941.

# Meeting of the Executive Committee

## WASHINGTON, D. C.

A stated meeting of the Executive Committee was held in the Board Room of the Cosmos Club, Washington, D. C., April 30, 1941. The meeting was called to order by President Ellery at 1.00 P.M. Present: President Ellery, Secretary Baitsell, Treasurer Pegram, Professors Lund, Shapley, Anderson, Jordan, Dr. Durand, Mr. Davies, and Mr. Sweet of the Alumni Committee. Among the important items of society business considered were the following:

1. REPORT OF THE PRESIDENT:

President Ellery presented a brief report of recent visits to twenty-three chapters and to the Sigma Xi Club at the University of Hawaii. It is planned to visit other chapters in the autumn. The President stated that important suggestions and recommendations are already being received from the chapters.

2. REPORT OF THE SECRETARY:

Secretary Baitsell reported various items which were deferred for consideration later in the meeting as arranged in the agenda.

3. REPORT OF THE TREASURER:

Treasurer Pegram presented the financial report for 1940 (Published in the QUARTERLY, April, 1941) and a proposed budget for 1941. After careful consideration it was

*Voted:* To adopt a budget of $14,906 for 1941.

It was further

*Voted:* That the consideration of the annual budget of the society be made a permanent item of the agenda at the December meeting of the Executive Committee.

The question of expenses incurred by members of the Executive Committee in attendance at the December meeting was considered, and it was

*Voted:* To recommend to the 1941 convention that the entire expenses of the members in attendance at this meeting be paid by the Society. (See By-Laws, Section III, page 33 of the "History and Constitution.")

The Committee consisting of the President, Secretary, and Treasurer appointed at the December 1940 meeting to consider the allocation of surplus funds presented their report which may be summarized as follows:

*a.* The Committee feels that the present surplus is not too large in comparison with the size of the annual budget.

*b.* The Committee feels that the accumulation of additional annual surpluses above a maximum amount of $1,000.00 is not desirable and suggests the following possibilities for using surplus funds should such accumulate in any fiscal year.

*i.* An increase in the total amount awarded for grants-in-aid for research.

*ii.* The award of two large national Sigma Xi fellowships (physical sciences; biological sciences). These might be awarded by the fellowship committee established by the National Research Council, since the council has already established the machinery for selection of candidates.

*iii.* The award of annual Sigma Xi prizes on somewhat the same basis as was done at the Semi-Centennial in 1936. If these prizes were awarded in connection with the annual Sigma Xi lecture, they might be an incentive to a larger attendance at the meeting.

*iv.* An extension of the national lectureships either by securing more lecturers or by increasing the number of engagements by each lecturer.

*v.* An increase in the budget of the QUARTERLY as was suggested in the report of the Richtmyer Committee.

4. INFORMAL PETITIONS FOR THE ESTABLISHMENT OF CHAPTERS:

Detailed consideration was given to informal petitions for the establishment of

chapters at a considerable number of institutions. It was

*Voted:* To ask the petitioning group of each of the following institutions to prepare formal printed petitions for submission to the national organization.

Louisiana State University, Utah State Agricultural College, Illinois Institute of Technology, University of Hawaii (provided certain deficiencies in the informal petition are satisfied).

5. Further Inquiries About the Establishment of Chapters:

Consideration was also given to the conditions existing in the following institutions with reference to chapter establishments, and the appropriate measures were taken in each case.

University of Georgia, Texas Technological College, University of Vermont, Marquette University, Emory University, Polytechnic Institute of Brooklyn, Tufts College, University of Denver, and Wayne University.

6. The Situation with Reference to Development of Science at the University of Oregon and its Effect on Sigma Xi at That Institution:

For some years the Executive Committee has been deeply concerned with the unsatisfactory situation at the University of Oregon resulting from the removal of the major portion of work in science to the Oregon State College at Corvallis. After full and detailed discussion it was

*Voted:* To recommend to the 1941 convention that the chapter of Sigma Xi at the University of Oregon be revoked: this action effective until such time as, and in the hope that, the institution will again be able to carry on work of university grade in the sciences. Furthermore, the action is taken through no fault of the loyal members of the Sigma Xi chapter at the University of Oregon.

7. Installation at Oberlin College:

The installation of the Oberlin chapter of Sigma Xi on March 12, 1941 was reported. The President and Secretary acted as installing officers.

8. Accrediting of Institutions by the American Association of Universities and Engineer's Council for Professional Development:

The Secretary reported on conferences which he had held with Dean A. A. Potter of Purdue University of the E. C. P. D., and with Dean Fernandus Payne of Indiana University of the A. A. U. on problems of accrediting. President Robert Doherty of Carnegie Institute of Technology was present at the Executive Committee meeting as a representative of the E. C. P. D. The matter may be summarized by the statement that both these organizations are willing to cooperate with Sigma Xi in such questions of accrediting as may arise.

9. Reports of Committees:

*a.* Committee on Grants-in-Aid.

The Secretary announced that approximately $3,000.00 had been received to date from the 1941 circularization of the Alumni. The Committee asked that a letter be sent to the Chapter Secretaries calling their attention to the availability of Sigma Xi grants-in-aid. The possibility of Sigma Xi grants-in-aid to foreign scientists was considered and referred to the Committee on grants-in-aid. The Secretary was instructed to secure reports from grantees for the past two years with a view to publication, either as a separate pamphlet or in a suitable periodical.

*b.* Nominating Committee.

The President asked for recommendations for a third member of the Nominating Committee.

10. Sigma Xi Quarterly:

The Secretary announced that the first of the national Sigma Xi lectures to be published in the Quarterly, "Image Formation By Electrons," by V. K. Zworykin, was being published in the Spring Number.

Consideration was given to the question of the possible change of the title of the Quarterly. Various members of the Committee expressed the belief that the present

title might be retained, with an addition of a possible chonge of the title of the periodical.

11. Proposed Study of Honor Societies:

The Secretary reported on a conference suggested by Dr. William Shimer, National Secretary of Phi Beta Kappa, with regard to a proposed study of Honor Societies in the educational institutions of this country. The Committee requested the Secretary to continue the conferences with Dr. Shimer. It was

*Voted:* To state that the Executive Committee is in favor of cooperating with Phi Beta Kappa on the proposed study, with the understanding that any report of the joint committee is to be submitted for the approval of the Executive Committee before publication.

12. Relations with the A. A. A. S.:

An invitation has been received from the A. A. A. S. asking for the cooperation of Sigma Xi at the summer meeting of the Association in Durham, New Hampshire in June, and Chicago in September. The President was requested to make such arrangements as may seem advisable for participation at the Durham meeting, and Mr. D. H. Sweet of the Alumni Committee was asked to explore the posssibilities of alumni participation at the Chicago meeting.

13. Sigma Xi Clubs:

It was announced that approximately half of the registered clubs had paid their membership assessment for 1941. It was the opinion of the Committee that alumni members who become club members of some institution, should not be expected to pay dues to the chapter where they were originally initiated. The Secretary announced that consideration was being given to the inauguration of a more formal procedure for the establishment of Sigma Xi Clubs.

14. Membership Problems:

Various problems relative to the eligibility of students in architecture and social sciences were considered by the committee: also suggestions from chapters relative to the various classes of members. They were referred to the Committee on Membership Structure.

# Contributors to Alumni Research Fund—1941

(Continued from the Spring number of the Quarterly. Total received to date is approximately $3,475, or about $700 more than last year.)

Everett L. Saul (Columbia)
William H. Sawyer, Jr. (Cornell)
C. F. Schenck (Columbia)
Francis R. Scherer (Michigan)
Melvin H. Schlesinger (Nebraska)
J. C. Schmidt (Nebraska)
Walter A. Schmidt (California)
Stuart L. Schoff (Ohio State)
Alfred R. Schultz (Chicago)
Ernest R. Schulz (Illinois)
M. M. Schwarzschild (Columbia)
Arthur R. Schweltzer (Chicago)
Dr. David Seecof (Colorado)
Joseph Segel (Kansas)
P. H. Senn (Florida)
Arthur H. Senner (Johns Hopkins)
H. A. Shabaker (Minnesota)
S. Paul Shackleton (Michigan)
George D. Shafer (Stanford)
Howard M. Sheaff, M.D. (Chicago)
John J. Sheinin (Northwestern)
J. Leon Shereshefsky (Johns Hopkins)
R. B. Sherman (Ohio State)
Miles S. Sherrell (M. I. T.)
Lloyd P. Shildneck (Nebraska)
Richard E. Shope (Princeton)
Barton P. Sibole (Penn.)
Lawrence B. O. Silverberg (Worcester)
F. A. Simeone (Brown)
Nina Simmonds (Johns Hopkins)
O. C. Simpson (Carnegie Tech.)
Cora P. Sletten (Chicago)
R. G. Sloane (Columbia)
Edward E. Slowter (Ohio State)
Charles H. Smith (Stanford)
Christianna Smith (Cornell)
Dr. Frederick L. Smith, 2nd (Pittsburgh)
Harold DeWitt Smith (Lehigh)
Leon E. Smith (Penn.)
F. E. Smyser (Ohio State)
Foster Dee Snell (Columbia)
H. D. Snively (Cincinnati)
Laetitia M. Snow (Chicago)
W. T. Snyder (Purdue)
Dr. LeRoy D. Soff (Columbia)
Ralph D. Spalding (Rensselaer)
W. M. Stanley (Princeton)
Naomi A. Stark (Colorado)
Ann D. Stautz, M.D. (Michigan)
Theron David Stay (Case)
Mary M. Steagall (Chicago)
Noel H. Stearn (Wisconsin)
Eunice Stebbins (Cornell)
Harold H. Steinour (C. I. T.)
Edward P. Stengle (Yale)
W. B. Stephenson (Purdue)
Alfred Still (Purdue)
Edward Kerth Stocker (Purdue)
S. H. Stoner (Purdue)
Lillian B. Storms (Columbia)
Frank J. Studer (Union)
Herbert Sturz (Stanford)
Charles S. Sulton (Brown)
Carl L. Svensen (Ohio State)
S. T. Swallow (Worcester)
Frank E. Swindells (Penn.)
George F. Sykes (Brown)
H. A. Taber (Brown)

Benjamin Tager, M.D. (Yale)
Mignon Talbot (Ohio State)
Edwy L. Taylor (Yale)
Hugh S. Taylor (Princeton)
John O. Taylor (Illinois)
M. H. Teaze (Worcester)
L. A. G. ter Veen (Illinois)
Samuel R. Thomas (Rensselaer)
Dr. Clara Thompson (Brown)
Helen B. Thompson (U. C. L. A.)
J. Trueman Thompson (Johns Hopkins)
E. G. Thomssen (Columbia)
Walter D. Tiedeman (Union)
S. G. Tilden (Penn.)
Elizabeth W. Towle (Chicago)
Martha Tracy (Penn.)
W. A. Trayler, Jr. (Purdue)
Henry W. Troelsch (Penn.)
H. M. Trueblood (Penn.)
R. V. Truitt (Maryland)
Frederick B. Utley (Yale)
Allen F. Van Alstyne (Rensselaer)
James T. Van Artsdalen (Penn.)
Charles B. Vance (Indiana)
Ralph G. Van Name (Yale)
Willard G. Van Name (Yale)
Lena Vaughan (Chicago)
F. K. Vaughn (Michigan)
Collins Veatch (Illinois)
John K. Vermard (N. Y. U.)
Edward C. Wach (Illinois)
B. L. Wade (Wisconsin)
Ruth Wall (California)
W. L. Wallace (Cornell)
Roscoe A. Weaver (California)
S. A. Weisman, M.D. (Minnesota)
W. L. A. Wellbrock, M.D. (Mayo)
Miriam Welles Reeves (Illinois)
E. L. West (Cornell)
Edward T. Wherry (Penn.)
Jessie Whitacre (Chicago)
M. W. White (Penn. State)
Virginia B. White (Missouri)
William C. White (Cornell)
Dr. John C. Whitehorn (Harvard)
E. E. Whiteley (Minnesota)
Paul L. Whitely (Chicago)
W. R. Whitney (Union)
Maurice Whittinghill (Michigan)
W. E. Wickenden (Case)
Alice Wilson Wilcox (Brown)
Levi Wilcox (Yale)
Edwin A. Wilde (Cornell)
H. D. Wilde (Texas)
Dorothy E. Williams (Columbia)
R. S. Williams (M. I. T.)
Samuel B. Williams (Ohio State)
Warren B. Williams (Michigan)
Dr. N. W. Winkelman (Penn.)
C. C. Winterstein (Penn.)
W. B. Wilson (Missouri)
Charles G. Woodbury (Purdue)
Regina Woodruff (Kansas)
Sybil Woodruff (Iowa)
A. F. Woods (Nebraska)
Charles E. Woodward (Worcester)
George H. Worrall (C. I. T.)
Dr. Arthur W. Wright (Rensselaer)
Dr. Carroll S. Wright (Penn.)
Donald D. Wright (Yale)
Margaret Wylie (Cornell)
Louis Yager (Minnesota)
Rowland L. Young (Penn.)
F. P. Zimmerli (Michigan)
Charlotte Zimmerschied (Minnesota)

Olaf S. Aamodt (Minnesota)
Ernest G. Allen, M.D. (California)
B. B. Beckett (Cornell)
Elmer Bisbee (Minnesota)
James W. Brown (Duke)
W. Gordon Brown (Yale)
Donald F. Campbell, Jr. (Iowa)
Clifford C. Church (Stanford)
George R. Cowgill (Yale)
Lincoln C. Damsgard (California)
David E. Debeau (California)
F. Derbenwick (Stanford)
Armand J. deRosset (Wisconsin)
John F. Dodge (Univ. of So. Calif.)
Henry Dorsey (Iowa State)
P. D. Edwards (Indiana)
Paul L. Errington (Wisconsin)
J. H. Euston (Illinois)
Rose Finkelstein (Brown)
Arthur G. Gehrig (Illinois)
Milton T. Hanke (Chicago)
Norman A. Hansen (Illinois)
E. B. Hodge (Purdue)
H. M. Huffman (Stanford)
J. P. Jollyman (Stanford)
Ennis E. Jones (Purdue)
R. M. Jones (Chicago)
Eleanora B. Knopf (Yale)
Harry H. Laidlow, Jr. (Wisconsin)
James E. Lipp (C. I. T.)
Mrs. Bernice B. Marblestone (Kansas)
W. J. Maytham (Cornell)
Joseph L. Meyer (Northwestern)
Dr. R. S. Poor (Illinois)
Lawrence S. Potter (Worcester)
Chas. F. Scott (Yale)
Leo Shapovalov (Stanford)
William B. Singer (Oregon State)
Dr. A. B. Spalding (Stanford)
O. W. Swainson (Washington)
John O. Thomas (Stanford)
John H. Watkins (Iowa State)
Anna Kellman Whitchurch (Cornell)
P. D. Wilkinson (Iowa State)

Elmer W. Adams (Wisconsin)
James F. Adams (Columbia)
L. H. Adams (District of Columbia)
E. J. Baldwin (Idaho)
E. H. Barkmann (Kansas)
Lt. Ernest S. Bathke (Rensselaer)
K. L. Berry (Yale)
Francis D. Bode (C. I. T.)
Gilbert H. Cady (Illinois)
Alfred J. Carah (Stanford)
Joe H. Clark (Texas)
Charlton D. Cooksey (Yale)
Rachel Davida Dent (California)
J. William DePoy (California)
Mrs. Marguerite Dietrich (Northwestern)
Lawrence B. Dodds (California)
Jerome K. Doolan (Stanford)
Robert B. Flint (Yale)
Mrs. Louise B. Freeman (Chicago)
Virginia Gangstad (Illinois)
Clarence J. Goodnight (Illinois)
Robert H. Guiberson (Mass. State)
L. D. Hagenbook (Purdue)
J. B. Hershman (Indiana)
John C. Hessler (Chicago)
T. T. Job (Chicago)
L. E. Josselyn (Chicago)
Sherman O. Kessler (Purdue)
Arthur B. Lewis (Johns Hopkins)
Robert L. Lowry (Texas)
E. C. Manderfeld (Minnesota)
Orville E. May (Illinois)
F. Chaloner McNair (Yale)
Dalton Moomaw (Case)
Walter J. Nichter (Purdue)
Dr. J. R. Paul (Yale)
Harold A. Peterson (Iowa)
Dr. D. R. Porter (Iowa State)
Ernest Y. Robinson (Cornell)
William C. Rockwell (Stanford)
John J. Sampson, M.D. (California)
Harrison P. Smith (Stanford)
Florence B. Snyder (Illinois)
W. C. Stahl (California)
Douglas B. Sterrett (Yale)
A. J. Stirton (Maryland)
Dr. Margaret Tyler (Yale)
William A. Williams (Purdue)
L. W. Wing (Missouri)

Norman A. Abbott (Rensselaer)
R. J. Achatz (Purdue)
E. Beth Achenbach-Branch (Iowa)
D. W. Albert (Washington)
A. R. Ayers (Cornell)
Osborn Ayers (Rensselaer)
Roy M. Barnes (California)
Marston Bates (Harvard)
Arthur J. Bedell, M.D. (Rensselaer)
C. R. Benson (Stanford)
D. G. Bovee (Michigan)
Francis C. Bragg (Worcester)
George M. Brill (Cornell)
Elliott L. Buell (M. I. T.)
Paul R. Burch (Virginia)
Miss Frankie Byrne (Illinois)
Frances Carter (California)
C. S. Chaffee (Stanford)
George H. Clapp (Pittsburgh)
G. H. Clevenger (Stanford)
Charles W. Comfort, Jr., M.D. (Yale)
Melville T. Cook (Rutgers)
Joseph N. Cornell (Yale)
H. Marjorie Crawford (Minnesota)
Joseph Daniels (University of Washington)
C. E. Davies (Rensselaer)
W. J. Day (Cornell)
Edwin J. DeBeer (Penn.)
Charles H. Decater (Worcester)
C. E. de la Chapelle, M.D. (N. Y. U.)
G. H. Dell (Illinois)
Hyman Diamond (Princeton)
Howard Dingle (Cornell)
John H. Dingle (Harvard)
Paul B. Donovan (Chicago)
J. C. Evans (Washington University)
John W. Finch (Idaho)
Thos. Flemming, Jr. (Cornell)
Ellen Gloyd (Ohio State)
Dr. Winifred Goldring (Union)
Clarence J. Gomph (Cornell)
Walter S. Gordon, Jr. (University of Washington)
Frank C. Greene (Indiana)

B. F. Groat (Minnesota)
Ferdinand W. Haasis (Johns Hopkins)
Florence Hague (Illinois)
Wm. S. H. Hamilton (Yale)
H. Harold Hartzler (Rutgers)
John W. Hazen (California)
Homer H. Helmick (Chicago)
R. W. Henderson, M.D. (Iowa)
Louis G. Herrmann, M.D. (Cincinnati)
Helen J. Hubbell (Columbia)
J. A. Hummel (Minnesota)
Willis R. Hunt (Yale)
Albert H. Huntington (Cornell)
H. Louis Jackson (Kansas)
Stanley Johnston (Michigan State)
Lloyd B. Jones (Cornell)
Howard U. Keenan (Purdue)
Rockwell M. Kempton (Michigan)
T. E. Kihlgren (Yale)
Frances Krasnow (Cornell)
Ralph C. Kahle, M.D. (Iowa)
Theodore Kyne (Yale)
Newton Lamb (Michigan)
Louis Lewon (California)
Irving G. Loxley (Brown)
Charles M. Lubcke (University of Washington)
Maude F. Lyon (Minnesota)
Harold L. Lyon (Minnesota)
Dr. V. W. McCorty (Kansas)
William W. Mein (California)
A. S. Merrill (Chicago)
H. R. J. Meyer (Cornell)
Harold Michener (California)
Philip Miller (Yale)
Ralph L. Miller (Ohio State)
Nathan Millman (Brown)
William W. Moore (C. I. T.)
Stuart Mudd (Washington University)
W. W. Nedrow (Nebraska)
Walter K. Nelson (Brown)
M. Graham Netting (Pittsburgh)
Dr. Mildred R. Newlin (Ohio State)
W. W. Nichols (Yale)
Paul T. Nims (Michigan)
J. M. Olin (Cornell)
Paul E. Packer (California)
Henry W. Parker (Penn.)
Vernon L. Parks (Rochester)
Samuel J. Pearlman, M.D. (Chicago)
Alfred Perkins (Johns Hopkins)
Garson Prenner (Michigan)
Walter P. Reid (Pittsburgh
William E. Reid (Columbia)
A. R. Rogowski (M. I. T.)
C. E. Rose (Rensselaer)
P. B. Sawn (Brown)
George G. Schaut (Penn.)
W. G. Schulte (Colorado)
Lenher Schwerin (Wisconsin)
Florence F. Scoular (Iowa)
Dennis Smith (Michigan)
Stanley Smith (Penn.)
J. W. Snyder (Cornell)
Walter H. Stainton (Cornell)
H. R. Straight (Illinois)
J. J. Thalheimer (Case)
Mrs. Selma C. Therriault (Minnesota)
P. W. Thompson (Cornell)
James D. Trask (Yale)
Eleanor M. Tucker (Smith)
S. S. Visher (Chicago)
Thos. H. Wackenden (Michigan)
Mable R. Walter (Illinois)
Howard S. Warren (Stanford)
Lucy J. Watt (Syracuse)
George W. Watts (Illinois)
M. A. Wilcox (Cornell)
Alan F. Williams (Cornell)
Rex B. Wilsey (Rochester)
Opal M. Wolf (Wisconsin)
Dr. David A. Wood (Stanford)
Donald G. Wood (Northwestern)
A. E. Woodward (Michigan)
Robert W. Young (University of Washington)

(*To be continued*)

# Dayton C. Miller

(*Concluded from page 143*)

dancing light beam. And the equation of the curve proved it to contain only a fundamental note and its harmonies. It was the curve of such a note as might linger at the close of an overture.

Dayton Miller died in Cleveland on February 22. He was beloved by student and colleague. He was known the world over for experiments in ether drift. He had one of the world's greatest collections of flutes. But to one who saw him only once there remains the memory of a white-haired man, a flute poised gently against his lower lip, while facile fingers moved nimbly over the keys, and of clear pure notes that had been accurately described in the language of mathematics, a harmony of beauty in sound and line, and a vibrating column of air made visible by a brilliant understanding mind.

© Bachrach

Perrin H. Long